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VOLUME LXXXVII

TIPHIA (HYMENOPTERA) OF AMERICA NORTH OF MEXICO: KEY TO SPECIES, DESCRIPTIONS OF SIX NEW SPECIES, AND NOTES ON SYNONYMY

BY H. W. ALLEN [1]

Moorestown, New Jersey

Species of *Tiphia* exhibit such marked antigeny that characters used to separate the species of one sex either do not occur in or are of no value in separating the opposite sex. Therefore, it is practically certain that there are errors in some of the existing associations. There are also numerous instances in which one sex is known but not the other. It follows that some of the described species are the opposite sex of species previously described. Obviously, these errors cannot be corrected until structures common to both sexes are discovered, or the relationship is clearly established by taking the two sexes while mating, or breeding males from known females, or collecting a large series including both sexes, living in close association. Males also have more sharply defined characters, and more species of this sex are recognized, so it follows that in the following key, the females of more

[1] The author gratefully acknowledges the helpful assistance of K. V. Krombein who carefully reviewed this paper and made many suggestions incorporated in it.

than one closely related species may run to one point. In general the terminology used in this paper follows that described and illustrated by Allen and Jaynes (Proc. U. S. Nat. Mus. 76, art. 17, 1930).

This paper does not include all the North American species which have been described, but merely those that the author is able to recognize. It does not include the numerous species inadequately described by early authors, for which no types are known to exist, or for several western species of which there are types in the British Museum. It also does not include the several species described from the West Indies.

The ownership of the type material has been indicated by initials in parentheses, as follows: (A.N.S.P.) Academy of Natural Sciences of Philadelphia; (C.U.) Cornell University; (U.S.N.M.) United States National Museum; (I.N.H.S.) Illinois Natural History Survey; (M.C.Z.) Museum of Comparative Zoology, Harvard University.

Key to Males

1. Tegula scarcely longer than broad 2
   Tegula almost twice as long as broad (widespread in eastern U. S.) *transversa* Say
2. Fifth sternite without denticles or short transverse ridges laterally .. 13
   Fifth sternite with denticles or short transverse ridges laterally 3
3. Denticles of sternites usually small and inconspicuous, or if long and erect, then distinctly longer on the fifth than the fourth sternite .. 4
   Denticles of sternites long, erect, and of nearly equal size on the fifth, fourth, and third sternites (New Mexico, Arizona) *odontogaster* Viereck
4. Lateral extension of radial cell at most only equal to that of second cubital cell 8
   Lateral extension of radial cell exceeding that of second cubital cell .. 5
5. Impunctate medial stripe of sixth sternite with its sides parallel and not flanked by a conspicuous tuft of hairs 6
   Impunctate medial stripe of sixth sternite wedge-shaped with its apex directed anteriorly, and flanked with dense, upright hairs (widespread in eastern U. S., introduced) ..... *vernalis* Rohwer
6. Head, pronotum, mesepisternum, and abdominal tergites highly polished; cheek at least as wide as an antennal fossa 7
   Head, pronotum, mesepisternum, and abdominal tergites uniformly shagreened; cheek one-half as wide as an antennal fossa (uncommon, introduced) ..... *sternata* Parker

7. Primary punctures of mesepisternum small, not well-differentiated from the interspersed minute punctures; lateral extension of radial cell far exceeds that of cubital cell (widespread in eastern U. S.) *egregia* Viereck

Primary punctures of mesepisternum of moderate size, and well-differentiated from the interspersed minute punctures; lateral extension of radial cell only slightly exceeding that of second cubital cell (widespread in eastern U. S.) ..... *subcarinata* Malloch

8. Denticles of fifth sternite erect and spine-like 9

Denticles of fifth sternite appressed and transversely elongated 11

9. Pygidium with prominent lateral carinae bordering punctate portion (Washington, Nevada, Nebraska) ..... *bakeri* new species

Pygidium with no lateral carinae bordering punctate portion 10

10. Denticle of fifth sternite small but spine-like (Colorado, New Mexico) *occidentata* Malloch

Denticle of fifth sternite large, conspicuous, with smaller denticles on the two preceding sternites (Montana) ..... *montana* new species

11. First sternite of abdomen without minute punctures on its disc; transverse carina of pronotum on its lateral aspect not conspicuously elevated 12

First sternite of abdomen with numerous minute punctures on its disc; transverse carina of pronotum on its lateral aspect prominently produced (New Jersey) ..... *insolita* Allen

12. Front with numerous interspersed minute punctures extending upward near eyes to level of lowest ocellus (widespread in East, introduced) *popilliavora* Rohwer

Front without interspersed minute punctures on upper half (New York, Pennsylvania, introduced) ..... *asericae* Allen and Jaynes

13. Dorsum of first tergite not abnormally swollen; anterior aspect of second tergite sloping gradually to a constriction between tergites one and two 15

Dorsum of first tergite abnormally inflated; anterior aspect of second tergite abruptly declivous to the constriction separating it from first tergite 14

14. Disc of first sternite on its posterior half with dense, conspicuous, minute punctures; lateral extension of radial cell at most only slightly exceeding that of second cubital cell; side of pronotum with a distinct groove across its disc; preapical band of punctures of first tergite very narrow and deeply impressed on both its anterior and posterior margins (Illinois, Kansas, New York) ..... *similis* Malloch

Disc of first sternite on its posterior half polished impunctate; lateral extension of radial cell distinctly exceeding that of second cubital cell; side of pronotum without a distinct groove across its disc; preapical band of punctures of first abdominal tergite moderately wide, at least laterally, and not sunk below surface on its posterior margin (widespread in eastern U. S.) ..... *affinis* Malloch

15. First abdominal tergite without an anterior transverse carina or sulcate break in the contour 19
    First abdominal tergite with an anterior transverse carina or sulcate break in the contour 16
16. Lateral extension of radial cell exceeding that of second cubital cell .. 18
    Lateral extension of radial cell distinctly less than that of second cubital cell 17
17. Posterior aspect of propodeum usually with conspicuous anastomosing rugulae; areola usually with convex sides (widespread in eastern U. S.) ..... *convexa* Allen
    Posterior aspect of propodeum without rugulae, or if present, only weakly so near transverse carina; areola usually with straight sides (widespread in eastern U. S.) ..... *infossata* Allen
18. Radial and cubital cells elongated; lateral extension of radial cell much exceeding that of second cubital cell; clypeal extension sharply bidentate (Florida, North Carolina, Virginia, New Jersey) *floridana* Robertson
    Radial and cubital cells not notably elongated; lateral extension of radial cell only slightly exceeding that of second cubital cell; clypeal extension with its apex slightly emarginate (widespread in eastern U. S.) ..... *illinoensis* Robertson
19. Lateral extension of radial cell at most only equal to that of second cubital cell 21
    Lateral extension of radial cell exceeding that of second cubital cell; second abscissa of cubitus joining radius far from apex of radial cell 20
20. Lateral extension of radial cell much exceeds that of second cubital cell; third tergite with larger punctures of disc widely separated, shallow and much larger than the other punctures (widespread in eastern U. S.) ..... *inaequalis* Malloch
    Lateral extension of radial cell only slightly exceeds that of second cubital cell; third tergite without conspicuously enlarged, shallow, and widely separated punctures (widespread in eastern U. S.) *conformis* Malloch
21. Preapical band of punctures of first abdominal tergite narrow, and deeply impressed, its punctures medially not visible, or if so not discrete; hind coxa with a carina between ventral and inner surfaces; hind tibia with a prominent linear, polished rib extending its entire length 31
    Preapical band of punctures of first abdominal tergite more than one puncture wide, and not deeply impressed; hind coxa without a carina between ventral and inner faces; hind tibia without a bare polished rib, or if present, it fades out on basal portion 22
22. Apex of clypeal extension not abnormally wide, and not extending laterally beyond outside edge of antennal fossa 23

Apex of clypeal extension abnormally wide, truncate, extending laterally beyond outside edge of antennal fossa (widespread in eastern U. S.) ..... *letalis* Roberts

23. Mandible lacking a cusp or tooth on upper margin, or if present, weakly developed 25

Mandible with a prominent cusp on upper apical margin 24

24. Sixth sternite with a tuft of long, erect, yellowish hairs which are much longer than adjacent hairs; hairs of body generally fine and short; apical extension of clypeus scarcely longer than diameter of an antennal fossa; primary punctures of front well-differentiated from the secondaries, and widely separated (widespread in eastern U. S.) *micropunctata* Allen

Sixth sternite without a conspicuous tuft of long, erect, yellowish hairs; hairs of body generally coarse and long; apical extension of clypeus distinctly longer than diameter of antennal fossa; primary punctures of front not well-differentiated from the secondaries, and contiguous over much of the area (widespread in eastern U. S.) .. *atlantis* Allen

25. Dorsum of pronotum laterally with secondary punctures less numerous than the primaries 26

Dorsum of pronotum laterally with secondary punctures much more numerous than the primaries (midwestern U. S.) .. *vulgaris* Robertson

26. Transverse carina of pronotum complete and strongly developed ... 29

Transverse carina of pronotum at most weakly developed, and lacking medially 27

27. Angulation of first abscissa of radius two-fifths its length from stigma 28

Angulation of first abscissa of radius one-sixth its length from stigma; mesepisternum with primary punctures of moderate size, separated on disc by many interspaces as wide as their average diameter, secondary punctures on its disc less numerous than primaries (widespread in eastern U. S.) ..... *rugulosa* Malloch

28. Mesepisternum with its primary punctures unusually large, everywhere contiguous, secondary punctures on its outer disc more numerous than the primaries (North Carolina) ..... *crassipunctata* Allen

Mesepisternum with its primary punctures of moderate size, and with many interspaces wider than the punctures, secondary punctures on its outer disc much less numerous than the primaries (California) *shastensis* Krombein

29. Posterior aspect of propodeum without rugulae, or if present only weakly so near transverse carina; areola usually with straight sides; side of propodeum on upper portion with 14 or more closely spaced rugae 30

Posterior aspect of propodeum with prominent longitudinal rugulae; areola usually with convex sides; side of propodeum on upper portion with 8 to 12 strong rugae (widespread in eastern U. S.) *convexa* Allen

30. Sixth sternite at its tip medially with a sparse tuft of long white, nearly erect hairs; side of propodeum finely shagreened (widespread in eastern U. S.) ..... *infossata* Allen
    Sixth sternite at its tip medially without a well-developed tuft of long, suberect hairs; side of propodeum coarsely, dull shagreened (North Carolina) ..... *dryophila* Krombein
31. Clypeus with its lateral carina not as described below 32
    Clypeus with its lateral carina extended straight, thin, and sharp to apex of denticle, overhanging the lateral pit, and the abruptly depressed and much retracted lateral margin (widespread in eastern U. S.) ..... *jaynesi* Allen
32. Hind basitarsus on inner face at most with a short, inconspicuous, polished carina; clypeal extension with denticles separated by a moderate emargination which is not deeply depressed at middle, apex with a well-defined polished impunctate band 33
    Hind basitarsus on inner face with a conspicuous, longitudinal, polished carina; medial extension of clypeus conspicuously bidentate, without a clearly defined impunctate apex (Florida) *irfla* new species
33. Abdominal tergites two to five with discal punctures only moderately enlarged 34
    Abdominal tergites two to five with discal punctures exceptionally enlarged, shallow, and dimpled (Arizona) ..... *tempeae* new species
34. Tegula with a groove on lateral margin (northeastern U. S.) *relativa* Viereck
    Tegula without a groove on lateral margin (widespread) *intermedia* Malloch

Key to Females

1. Hind basitarsus on inner face with a longitudinal groove 10
   Hind basitarsus on inner face without a groove 2
2. Tegula scarcely longer than wide 3
   Tegula nearly twice as long as wide (widespread in eastern U. S.) *transversa* Say
3. Pygidium punctate at most on slightly more than basal half 6
   Pygidium punctate on basal three-fourths or more 4
4. Prosternum without dense minute punctures on disc 5
   Prosternum with dense minute punctures on disc (midwestern U. S.) *vulgaris* Robertson
5. Clypeus with its median extension elongated to one and one-third times diameter of an antennal fossa (Georgia) ..... *unica* Allen
   Clypeus with its median extension shorter than diameter of an antennal fossa (Missouri) ..... *raui* Allen
6. First tergite with a broad patch of dense, conspicuous minute punctures on anterior aspect 8

First tergite with minute punctures on anterior face occurring either as a narrow patch near its base, or as a broad patch in which the punctures on its periphery are widely separated 7

7. Clypeus with its lateral margin abruptly retracted beneath the strong, overhanging lateral carina; mandible of moderate length, with its lower blade expanded to make the apical half of the mandible trowel-like (widespread in eastern U. S.) ..... *letalis* Roberts

Clypeus, when viewed from the front, with its lateral margin and lateral pit not overhung by the lateral carina at any point; mandible long, slender and the apical half not abruptly expanded (widespread in eastern U. S.) ..... *confusa* Allen

8. Cubital cell elongate, about twice as long as greatest width 9

Cubital cell unusually short, being 1.3 times as long as greatest width (West Virginia) ..... *indistincta* new species

9. First tergite with its patch of dense minute punctures extending laterally to edge of lateral patch of minutes; preapical band of punctures fine, not impressed, and distributed as a thin line scarcely more than one puncture wide; punctures of intermediate tergites unusually small (widespread in eastern U. S.) ..... *micropunctata* Allen

First tergite with its patch of dense minute punctures bordered laterally by an area of coarse primaries; preapical band of moderate-sized punctures, 2 to 3 punctures wide; punctures of intermediate tergites moderately coarse (widespread in eastern U. S.) ..... *infossata* Allen

10. First tergite without a transverse carina 12

First tergite with a transverse carina at anterior edge of dorsal aspect 11

11. Clypeus polished impunctate one-half distance to base of antennae; groove on hind basitarsus deep and long (widespread in eastern U. S.) ..... *pennsylvanica* new species

Clypeus with its apical extension coarsely punctate to apex; groove on hind basitarsus shallow and scarcely one-third length of the joint (North Carolina) ..... *incisurata* Malloch

12. Pygidium rugose-punctate on anterior three-fifths or less 13

Pygidium rugose-punctate to apical margin (Florida, New Jersey) *floridana* Robertson

13. Pygidium with its impunctate apex at most only finely shagreened near the punctate portion 15

Pygidium with its impunctate apex broadly and conspicuously shagreened 14

14. Large species with unusually small eyes; pygidium with its apex broadly subtruncate and upcurled (Nevada, California) .. *tegulina* (Malloch)

Small species with eyes of normal size; pygidium at apex pointed and not upcurled (widespread in eastern U. S.) ..... *rugulosa* Malloch

15. Preapical band of punctures of first tergite usually narrowly linear and often impressed over much of the dorsum 24

Preapical band of punctures of first tergite two or more punctures wide over much of the dorsum, and not impressed 16

16. Moderate-sized to large species 19
    Small species, 4.5 to 8 mm. 17
17. Tegula and legs red; stump of radius at apex of second cubital cell outwardly directed 18
    Tegula and legs black; radius without a well-defined apical stump; tergites 2, 3, and 4 with apical rows of microscopic incisions continuous over the dorsa (North Carolina) ..... *dryophila* Krombein
18. Contact between bare, lower, inner face of hind tibia and upper hairy area perceptibly elevated (Illinois) ..... *aterrima* Malloch
    Contact between bare lower inner face of hind tibia and upper hairy area not perceptibly elevated
    { (widespread in East) ..... *egregia* Malloch
    { (Nebraska, California) ..... *diminuta* Roberts
19. Stump of radius at apex of second cubital cell directed outward ... 21
    Stump of radius at apex of second cubital cell directed inward toward costal margin, or the knot-like enlargement of nervure much laterad of anterior apex of second cubital cell 20
20. Tegula with a marginal groove on outside, and opaque black except on margin; dorsum of propodeum with lateral sulcus subobsolete; sensorium of hind tibia reddish (widespread in eastern U. S.) *atlantis* Allen
    Tegula without a marginal groove on outside, thin, translucent red; dorsum of propodeum with a lateral sulcus developed almost to spiracle; sensorium of hind tibia black, bordered by red (introduced and widespread in eastern U. S.) ..... *popilliavora* Rohwer
21. Hind tibia on inner face smoothly contoured without any sharp separation between upper and lower portions 22
    Hind tibia on inner face with lower half polished and raised on a sharp line of contact with the upper hairy portion; distance between posterior margin of buccal cavity and occipital carina one-fourth to one-third length of buccal cavity; tegula without marginal groove; lower portion of side of propodeum uniformly shagreened; punctate portion of pygidium with a broad, smooth impunctate emargination (widespread in eastern U. S.) ..... *robertsoni* Malloch
22. Lateral sulcus on dorsum of propodeum with its inner carina obsolete; impunctate apex of pronotum medially without minute longitudinal creases; median carina of posterior aspect of propodeum obsolete .. 23
    Lateral sulcus on dorsum of propodeum with parallel and equal bordering carinae; impunctate apex of pronotum medially with a minute longitudinal crease, or creases; medial carina of posterior aspect of propodeum usually complete to transverse carina (introduced and widespread in eastern U. S.) ..... *vernalis* Rohwer
23. Side of propodeum uniformly shagreened; distance between margin of buccal cavity and occipital carina not exceptionally narrow; propodeum with transverse carina lacking at apex of areola; sensorium of hind tibia very large (California) ..... *shastensis* Krombein

Side of propodeum not shagreened, microscopic setigerous punctures the dominant sculpturing; distance between margin of buccal cavity and occipital carina narrow, scarcely one-fourth length of cavity; propodeum with transverse carina complete at apex of areola; sensorium of hind tibia very small (widespread in eastern U. S.) *conformis* Malloch

24. First tergite usually without a well-defined patch of minute punctures on anterior aspect, or if minute punctures are present, the tegula is not conspicuously shagreened, or the apex of the abdomen abnormally extended 26

First tergite with a conspicuous elongate median patch of well-differentiated secondary punctures, sometimes extending almost to the preapical band 25

25. Third abdominal tergite with its non-membranous apex medially impunctate for a distance twice as great as the diameter of the larger adjacent primary punctures; notauli and anterio-medial groove continuous (Illinois) ..... *arida* Malloch

Third abdominal tergite with its non-membranous apex medially impunctate for a distance scarcely equal to diameter of adjacent primary punctures; notauli and anterio-median groove not continuous (Texas) ..... *texensis* Malloch

26. Groove on inner face of hind basitarsus long, deep, and never vestigial 28

Groove on inner face of hind basitarsus short, shallow, vestigial 27

27. Preapical band of punctures on first tergite deeply impressed; groove across side of pronotum a series of faint coalesced aciculations; apical stump of radius, if present, not directed outwardly; medial carina of posterior aspect of propodeum confined to lower half or less (New York, Pennsylvania, introduced) ..... *asericae* Allen and Jaynes

Preapical band of punctures of first tergite linear medially but not impressed; groove across side of pronotum linear and unbroken on a smooth disc; apical stump of radius directed outwardly; medial carina of posterior aspect of propodeum complete to transverse carina (introduced but uncommon) ..... *sternata* Parker

28. Clypeus with its median extension strongly emarginate or bidentate 29

Clypeus with its median extension arcuate; side of propodeum uniformly shagreened (widespread in eastern U. S.) .. *robertsoni* Malloch

29. Clypeus with its median extension emarginate, the emargination not strongly depressed, apex broadly polished impunctate 31

Clypeus with its median extension bidentate, the area between the denticles strongly depressed, apex coarsely punctate 30

30. Mesepisternum and front with punctures contiguous and exceptionally coarse; anterior carina of mesepisternum unusually high (Florida) *irfla* new species

Mesepisternum and front with medium-sized punctures, well-spaced; anterior carina of mesepisternum of normal height (widespread in eastern U. S.) ..... *clypeolata* Malloch

31. Tegula without a groove or linear depression on outer margin 32
Tegula with a groove or faint depression on outer margin (northeastern U. S.) ..... *relativa* Viereck

32. Fourth abdominal tergite with a broad lateral impunctate area; impunctate apex of pygidium at most only faintly shagreened (widespread) ..... *intermedia* Malloch
Fourth abdominal tergite without a broad lateral impunctate area; impunctate apex of pygidium more distinctly shagreened (widespread in eastern U. S.) ..... *jaynesi* Allen

Tiphia irfla new species

Tiphia irfla is related to *T. intermedia* Malloch.

Holotype.—♂; Indian Rock, Florida, Aug. 21, 1931, collected by Bradley and Knorr (C.U.).

Male.—Clypeal extension strongly bidentate, the distance between points slightly shorter than the clypeo-antennal distance; scarcely impunctate; disc flattened; lateral carina conspicuous and broadly overhanging the deeply recessed lateral pit. Cheek only slightly wider than an antennal fossa. Primary punctures of front very coarse, and contiguous to level of lowest ocellus; interspersed with a few secondary punctures.

Pronotum with transverse carina uniformly high; punctures very coarse, nearly contiguous, and extending medially to beyond anterior half. Side of pronotum with discal aciculations, those in middle broadened to an interrupted groove when viewed from in front. Mesepisternum with very coarse, contiguous punctures, the secondaries on the outer disc somewhat more numerous than the primaries. Coxa of hind leg with an obscure carina between ventral and inner face. Hind tibia densely hirsute except for a narrow, sharply defined, longitudinal ridge. Hind basitarsus with a well-developed longitudinal carina on inner face, extending from its base to near its apex. Tegula polished black, without a marginal groove. Wing hyaline; second cubital cell extending laterally slightly farther than the radial cell.

Dorsum of propodeum with its areola keystone-shaped and strongly tapering, slightly longer than greatest width; transverse carina strongly developed. First tergite without anterior transverse carina or sulcate break, with scattered, well-developed primary punctures which almost obliterate the usual dorsal impunctate area; preapical band of punctures deeply impressed, one puncture wide except for a few scattered doubles, the punctures well-differentiated. First sternite with lateral groove extending almost to escutcheon. Junction between first and second tergite conspicuously constricted. Intermediate tergites coarsely and rather uniformly coarse punctate without conspicuously enlarged punctures. Pygidium with a sharp

medial ridge extending to base of punctate portion.

Length, 9 to 10 mm.

Allotype.— ♀ ; same locality and date as type (C.U.).

Female.—Differs from the related *intermedia* as follows: Clypeal extension lacking an impunctate apex, conspicuously bidentate, the distance between point apices about equal to clypeo-antennal distance. Front with punctures much coarser and contiguous to above level of lowest ocellus. Mesepisternum with larger, contiguous punctures; anterior carina exceptionally high. Femora black. Dorsum of propodeum with the minute punctures on either side of areola more sparse and less conspicuous. First tergite with the transverse impunctate area anterior to the preapical band narrower and less clearly defined.

Length, 12 to 13 mm.

Paratypes.—6 ♂♂ and 7 ♀♀, Indian Rock, Florida, Aug. 21, 1931 (Bradley and Knorr); 1 ♂, St. Petersburg, Florida, Aug. 18–26, 1931 (Bradley and Knorr) (All C.U.). 2 ♂♂, Orange Co., Florida, June 17, 1929 (C. Nelson); 1 ♂, Orange Co., Florida, June 29, 1929 (B. D. Hiers, Jr.) (All U.S.N.M.).

I have also seen one female, Jacksonville, Florida (Ashmead).

Tiphia tempeae new species

This species has all the principal characters noted for *intermedia* except the punctation of the abdominal tergites. The largest punctures on tergites 3 and 4 are relatively much larger, more conspicuously dimpled. Their diameters are almost one-fifth the length of the punctate portion of the tergite. In *intermedia* the largest punctures are scarcely more than one-tenth the length of the punctate portion.

Holotype.— ♂ ; Tempe, Arizona, Aug. 4, 1917 (C.U.).

Male.—Front with coarse punctures nearly contiguous up to a distance equal to width of an ocellus from ocellar triangle, with sparse secondaries extending into upper half. Cheek wider than an antennal fossa. Clypeus with its median extension bidentate, apex of denticle below middle of antennal fossa, clypeal extension broadly polished impunctate and scarcely depressed between apices of denticles. Lateral carina weakly developed and not overhanging the shallow lateral pit. Mandibles simple.

Dorsum of pronotum with a strong transverse carina; punctures moderately large, thinning out on lateral discs, secondaries numerous anteriomedially. Side of pronotum polished, without a groove across its disc. Mesepisternum with punctures of disc fine and principally of third-degree density, secondaries more numerous than the primaries. Legs largely piceous to reddish. Hind coxa with a perceptible ridge between inner and

ventral faces. Hind tibia with a conspicuous, narrow, polished rib on its inner face. Hind basitarsus with a vaguely defined carina on its inner face. Tegula highly polished, piceous, without a marginal groove. Wing with lateral extension of radial cell almost equal to that of second cubital cell.

First tergite without an anterior transverse carina or sulcate break; dorsally with a wide, impunctate polished area; preapical band of punctures narrowly linear, deeply impressed, the punctures not discrete. Tergites 4 to 6, each with several very broad, shallow, dimpled punctures on its disc which are many times larger than the other primary punctures.

Length, 6 to 7 mm.

Female.—Unknown.

Paratypes.—7 ♂♂, Tempe, Arizona, Aug. 4, 1917 (C.U.).

Tiphia bakeri new species

This species differs from all others I have seen in having conspicuous carinae on either side of the punctate portion of the pygidium, frequently partly concealed beneath the thin, broad, translucent borders of the terminal sternite. I would also place here two males identified by Roberts as *diminuta* and included among his paratypes of that species. They appear to be practically identical with the type of *bakeri* except that they are a little smaller, being 6 mm. long. The type of *diminuta*, a female, and the female specimens seen by Roberts ranged a little smaller than the males, a most unusual situation in *Tiphia* where females generally average much larger than males. Therefore, I am of the opinion that the type series of *diminuta* females represent another, and smaller species. The type series of *bakeri* was collected many years ago, presumably in what is now the state of Washington.

Holotype.—♂; labelled "W.T." (A.N.S.P. Type no. 10702).

Male.—Front with primary punctures coarse, deep, closely contiguous, with widely scattered secondary punctures, and few interspaces as wide as the larger primaries. Clypeal extension strongly bidentate, impunctate only on dentate portion; lateral carina nearly absent and scarcely overhanging the very shallow lateral pit. Antenna black. Palpi brown.

Pronotum medially with primary punctures closely contiguous, medially with punctate portion fully twice as wide as impunctate apex. Side of pronotum with a broad area of strong rugae but no diagonal groove across disc. Disc of mesepisternum polished, almost without secondary punctures. Hind tibia with its sensorium linear, 4 to 5 times as long as wide, and with inner face uniformly hirsute and lacking a polished medial ridge. Tegula largely black, without marginal groove on outside around the alar

angle. Wings with radial cell equal to second cubital cell in lateral extension; an angular bend in the radius one-third distance to junction with first intercubital nervure; recurrent nervure joining cubitus slightly over half way between first and second intercubitals.

Dorsum of propodeum conspicuously reticulate; areola slightly longer than basal width, with sides concave and convergent toward apex, with median carina on anterior three-fourths. First tergite almost without minute punctures; dorsum moderately inflated; preapical band of punctures a series about 3 wide, only slightly impressed. First sternite with disc irregularly sculptured anteriorly, polished and nearly devoid of minute punctures apically; lateral groove on lower half. Abdominal tergites 3 to 5 with microscopic apical grooves continuous over the dorsum. Fifth sternite with a small, erect, subconical lateral denticle; other sternites without denticles. Pygidium rugoso-punctate, without a medial impunctate stripe, but rostrate apically; laterally with a carina bodering the punctures, which in repose is frequently concealed by the elevated side of the sixth sternite.

Length, 8 to 9 mm.

Female.—Unknown.

Paratypes.—5 ♂♂ with the same label as the type (A.N.S.P.); 4 ♂♂, Ormsby Co., Nevada, Cornell Univ. lot 546, sub. 6, Baker Collection.

One of the Nevada specimens also bears the number 3441, and an identification label "*Paratiphia nevadaensis* Cam.". This probably was identified by Cameron, but whether it is the same as the type of *nevadensis* is quite uncertain. It is not a *Paratiphia*.

Tiphia montana new species

This species has a larger and more conspicuous denticle on the fifth sternite than any other species I have seen. It appears to be closely related to *odontogaster*, but differs in having the denticles of the fourth and third sternites much smaller than that of the fifth. In *odontogaster*, the denticles of sternites 4 and 3 are almost as large and high as that of sternite 5, and the radial cell is about equal to the cubital cell in lateral extension.

Holotype.— ♂; labelled "Montana" (A.N.S.P. Type no. 10703).

Male.—Front broadly beset with coarse contiguous punctures except for small narrow spaces below each ocellus, and with sparse secondaries on upper half. Cheek much wider than an antennal fossa. Clypeus with its median extension at least a third longer than its apical width, strongly bidentate, only the denticle impunctate; lateral carina rather weak and not overhanging the shallow lateral pit. Mandible simple, or with an inconspicuous notch on upper margin near apex.

Dorsum of pronotum with its anterior portion coarsely and uniformly punctate with nearly contiguous punctures, secondaries nearly lacking; transverse carina usually present and complete. Side of pronotum aciculate on lower portion, without a groove across its disc. Mesepisternum with coarse punctures generally of second-degree density, secondaries on disc almost lacking. Legs black to piceous. Hind coxa without a carina between ventral and inner face. Hind tibia with an obscure polished stripe on inner face. Tegula black, with a very fine groove close to the margin. Wing with lateral extension of radial cell distinctly less than that of second cubital cell.

First abdominal tergite without an anterior transverse carina or sulcate break; preapical band consists of coarse discrete punctures, shallowly impressed, about 2 punctures wide at middle. Tergites 3 and 4 with sparsely punctate areas in which the punctures are moderately enlarged and dimpled. Sternites 5, 4, and 3, each with lateral denticles diminishing rapidly in size from the very large and erect spine on sternite 5 to an inconspicuous lateral ridge on sternite 3. Pygidium with a V-shaped median portion radiating from the terminal rostrum; sides without carinae bordering the punctate portion.

Length, 6.5 to 9 mm.

Female.—Unknown.

Paratypes.—9 ♂♂, also labelled "Montana" (A.N.S.P.).

I have also examined 8 others, more or less dilapidated specimens of the same series. Although the other characters appear to be quite constant, there is considerable variation in the sternal denticles. However, the denticle of the fifth sternite is always much larger than in *occidentata* or *bakeri*, and those of the other sternites smaller than in *odontogaster*. In some specimens the transverse carina of the pronotum is almost lacking.

Tiphia indistincta new species

This species differs from *micropunctata* and others of that group in having a distinctly shorter second cubital cell in which the apical sections of the cubitus are equal. The species is described from a single female specimen.

Holotype.—♀; Kanawha Sta., West Virginia, June 26, 1918, collected by S. A. Rohwer (U.S.N.M.).

Female.—Ocellar triangle 1.3 times as wide as ocellocular distance. Front with coarse, contiguous punctures on lower two-thirds. Clypeus with its median extension smoothly arcuate, impunctate about one-half distance to base of antennae; lateral pit lacking; lateral carina almost absent.

Dorsum of pronotum with transverse carina lacking. Side of pronotum without a groove across its disc. Tibiae of mid- and hind legs reddish. Hind basitarsus without a groove, and 6.5 times as long as middle width. Tegula with a marginal groove. Wing with second cubital cell unusually short, being 1.3 times as long as greatest width; third and fourth abscissae of cubitus are equal.

Areola slender, about 3 times as long as greatest width, sides slightly convergent below middle, apex broadly truncate. First abdominal tergite with a broad median patch of minute punctures on anterior aspect which is somewhat smaller than that of *micropunctata* and it is bordered on the side with scattered primaries; preapical band not impressed, and composed of fine punctures, one or two wide. Intermediate tergites with fine punctures about as in *micropunctata*. Pygidium punctate on basal half, with an obscure medial indentation, and shallow wrinkles caudad of punctate portion; apex polished, not shagreened.

Length, 13 mm.

Male.—Unknown.

Tena

Tiphia pennsylvanica new species

This species can be distinguished at once from most species of *Tiphia* by the presence of a well-developed transverse carina on the anterior dorsum of the first tergite. It is apparently more common and widespread than *incisurata* that also has this feature. It is probable that the opposite sex is one of the several species in which the male also has a transverse carina on the first tergite, but at present there is little evidence indicating which this might be.

Holotype.— ♀ ; labelled "Pa. 2151, C. F. Baker Collection" (U.S.N.M.).

Female.—Front with primary punctures on upper two-thirds mainly of second-degree density. Clypeus with its median extension slightly emarginate, its apex conspicuously polished impunctate one-half distance to base of antennae, its largest punctures relatively small and inconspicuous; lateral margin not abruptly declivous and, when viewed from in front, is overhung by lateral carina from a point farther laterad than the outside of the antennal fossa.

Dorsum of pronotum with coarse primary punctures, mainly of second-degree density; transverse carina sometimes complete, sometimes absent medially. Side of pronotum without a groove across its disc, but with fine aciculations on ventral half. Scutum with notauli and anterio-medial groove continuous, or nearly so. Legs black. Hind tibia with margin of bare inner face raised at line of contact with the densely hairy portion;

sensorium broad, black, concolorous with surrounding area. Hind basitarsus on inner face with a long, deep groove; terminal bristles not differentiated into a comb of short, stout spines of equal length. Tegula polished, without shagreening or marginal groove, black with piceous edges. Wings slightly infumated, nervures light brown.

Dorsum of propodeum with areola almost rectangular, broadly truncate at apex, but slightly constricted medially, bordered laterally by numerous obsolete punctures. Side of pronotum on lower half polished, faintly shagreened, posteriorly rather densely micro-setulose. First tergite with a transverse carina at the anterior margin of the dorsal aspect from which the anterior slope is abruptly declivous, with its micro-punctures confined to a small medial patch; preapical band of punctures not strongly impressed, one puncture wide on medial one-third, becoming two or more laterally. First sternite with lateral groove strongly continuous to escutcheon. Intermediate tergites with well-differentiated lateral impunctate spots; medially with non-membranous apices impunctate at least twice width of adjacent primary punctures on tergites 1, 2, and sometimes 3; the polished apices without single rows of minute punctures over the dorsum. Pygidium uniformly rugoso-punctate on basal three-fifths, with a distinct indentation of the punctate portion; apical portion faintly shagreened near punctures, polished apically.

Length, 10 to 14 mm.

Male.—Unknown.

Paratypes.—All ♀♀. 6, Baker Collection, Pennsylvania, 2029; 1, Stanton, Delaware, July 31, 1951 (D. F. Bray); 1, Creole, Louisiana; 3, Orange Co., Florida, Fruit Fly Trap Survey in 1929, 2 collected by J. E. Sadler, and 1 by C. J. Guard (All U.S.N.M.). 1, Gloucester Co., New Jersey, Aug. 13 (I.N.H.S.).

Tiphia atlantis Allen

Tiphia atlantis Allen, Trans. Amer. Ent. Soc. 60: 314–315, 1934.

This species was originally described from a female collected at New Lisbon, New Jersey. In 1934, R. H. White collected at Vincentown, New Jersey, a few miles from the type locality, a series of 9 females and 17 males between April 19 and 23, taking one pair in coitu. The following description of the male was made from this series. This appears to be one of the few native species to emerge early in the northern states.

Male.—Front with punctures contiguous upward to level of lowest ocellus; ocellocular distance more than twice greatest diameter of lateral ocellus. Cheek slightly wider than an antennal fossa. Clypeal extension flat, uniformly punctate almost to apex, which is subtruncate and not perceptibly upturned; lateral pit short but deeply impressed beneath lateral carina. Mandible black, with a strong cusp on upper margin.

Dorsum of pronotum with its transverse carina complete, but weak medially; punctate portion slightly longer than the impunctate apex. Side of pronotum with irregular aciculations diagonally across disc. Hind tibia without a carina or polished stripe on inner face; hind coxa not carinate between ventral and inner faces. Tegula with a faint marginal groove. Wing with radial cell not equalling second cubital cell in lateral extension.

Dorsum of propodeum with a patch of dense shallow punctures. First tergite with preapical band of punctures several punctures wide and not sharply impressed. Intermediate tergites with punctures rather uniform in size and distribution. Sternites without lateral denticles. Pygidium dorsally with a rounded, impunctate crest extending to its base; apex in side view broadly truncate to a point near tip of posterior clasper when it is in repose.

Length, 8 to 10 mm.

Tiphia relativa Viereck

Tiphia relativa Viereck, Ent. News 17: 304, 1906. Adams, Jour. Econ. Ent. 42: 628, 1949. Franklin, Mass. Agric. Exp. Sta. Bull. 445, pts. 2–7: 63, 66–67, 1950.

Tiphia winnemanae Malloch, Ill. Nat. Hist. Surv. Bull. 13: 23, 1918.

I have examined the type of *relativa*, a male collected at North Haven, Connecticut, at the Connecticut Agricultural Experiment Station, and the type of *winnemanae*, collected at Plummers' Island, Maryland (Banks), no. 10255 at the Museum of Comparative Zoology. I can find no characters sufficient to separate them as different species. In the type of *winnemanae*, the punctate portion of the pronotum is longer than the impunctate apex, the areola has a complete median carina, and the lateral groove of the first sternite is confined to the apical half, all characters variable within the species. This species, and especially the female, is not readily separated from *intermedia*. I have examined 7 pairs taken in coitu by H. J. Franklin at Carver, Massachusetts, July 20, 1931. The description of the female is based on this series.

Female.—Clypeus with its median extension subtruncate to bilobate, impunctate on apical half; lateral carina and underlying lateral pit extending mediad to a point below middle of antennal fossa.

Dorsum of pronotum with its transverse carina high and complete except

a narrow medial gap. Legs black. Hind basitarsus with a groove one-half its length; length of joint 4 times its middle width. Tegula black, polished, obscurely creased on lateral margin.

Dorsum of propodeum finely striate anteriorly, glossy caudally, with small, deep, widely scattered punctures on either side of areola; areola rectangular to slightly tapering, its median carina complete, nearly devoid of minute hairs. First tergite with a broad area on dorsum impunctate except for widely scattered punctures; preapical band of punctures usually impressed on posterior border, and consisting of discrete punctures about one puncture wide. First sternite with a narrow, well-defined lateral groove on apical half. Pygidium on basal three-fifths with sculpturing that is more rugose than punctate, the rugae continued in the impunctate portion as wrinkles; without a median indentation of the punctate portion; impunctate apex faintly and inconspicuously shagreened to near the tip which is smoothly rounded.

Length, 9 to 11 mm.

Tiphia micropunctata Allen

Tiphia micropunctata Allen, Trans. Amer. Ent. Soc. 60: 297, 1934.
Tiphia dentata Allen, Trans. Amer. Ent. Soc. 60: 303, 1934.

I now regard *dentata* as a synonym of *micropunctata*. As to characters previously used to separate them, I cannot now detect a well-marked difference in the first abdominal sternite, and while the marginal groove of the tegula of some of the type material of *dentata* is more distinct than that in typical specimens of *micropunctata*, and closer to the margin, this single character is not considered sufficient to distinguish them as separate species.

Tiphia illinoensis Robertson

Tiphia illinoensis Robertson, Trans. Amer. Ent. Soc. 27: 196, 1901. Malloch, Ill. Nat. Hist. Surv. Bull. 13: 24, 1918. Bradley (in Leonard), N. Y. (Cornell) Agric. Exp. Sta. Mem. 101: 992, 1928.
Tiphia waldenii Viereck, Ent. News 17: 302, 1906. Malloch, Ill. Nat. Hist. Surv. Bull. 13: 23, 1918. Allen, Trans. Amer. Ent. Soc. 60: 313, 1934.
Tiphia brunneicornis Viereck, Ent. News 17: 303, 1916. Allen, Trans. Amer. Ent. Soc. 60: 313, 1934.

Robertson described *illinoensis* from 32 male and 10 female cotypes from Carlinsville, Illinois. Although he was the first to note (in *floridana*) the transverse carina of the first tergite, an excellent diagnostic character, he made no mention of this character in his description of *illinoensis*. Malloch noted the presence of this transverse carina in several of the males of the type series, and removed several misidentified specimens which he determined as *intermedia*. Neither Malloch nor I have seen any of the females described by Robertson. I have seen a male of the

type series in the collection of the Illinois Natural History Survey labelled "Charles Robertson Collection 6294" which I hereby designate as the lectotype. I have also examined the male type of *waldenii* from North Haven, Connecticut in the collection of the Connecticut Agricultural Experiment Station, and consider it conspecific with *illinoensis*. The synonymy of *brunneicornis* has been previously noted.

Tiphia texensis Malloch

Tiphia texensis Malloch, Ill. Nat. Hist. Surv. Bull. 13: 9, 20, 1918. Frison, Ill. Nat. Hist. Surv. Bull. 16: 230, 1927.

I hereby designate as lectotype, a female in the collection of the Illinois Natural History Survey labelled "Dallas, Texas, type 10252, cotype ♀, *Tiphia texensis* Malloch."

Tiphia vulgaris Robertson

Tiphia vulgaris Robertson, Trans. Amer. Ent. Soc. 27: 195, 1901. Davis, Ill. Nat. Hist. Surv. Bull. 13: 69, 1919. Malloch, Ill. Nat. Hist. Surv. Bull. 13: 5, 6, 12, 1918. Allen, Trans. Amer. Ent. Soc. 60: 305, 1934.

I designate as lectotype, a male, no. 4386, Chas. Robertson Collection (now at Urbana, Illinois) collected at Carlinsville, Illinois May 25, 1887, on the flowers of *Heracleum lanatum*. Robertson described this species originally from 37 males and 8 females from Carlinsville, Illinois and Orlando, Florida. Of the females, I have seen only one of the type series, specimen 7663 of the Robertson Collection which is definitely not *vulgaris* as presently recognized, but *confusa* Allen. It is probable that this species does not occur in Florida.

Tiphia infossata Allen

Tiphia infossata Allen, Trans. Amer. Ent. Soc. 60: 301–302, 1934.
Tiphia hollowayi Allen, Trans. Amer. Ent. Soc. 60: 303–305, 1934.

In a letter dated Dec. 8, 1960, K. V. Krombein states that he is convinced that *hollowayi*, known only as the male, is the opposite sex of *infossata*, known only from the female. He arrived at this opinion after identifying specimens of both sexes collected at the same time and locality. The author has also identified specimens of both sexes taken at the same time and place at Urbana, Illinois in 1889, and also at LeRoy, Illinois on June 23,

1907. The type of *infossata* was taken at Moorestown, New Jersey, and of *hollowayi* at Langhorne, Pennsylvania, only about 15 miles from Moorestown.

Tiphia incisurata Malloch

Tiphia incisurata Malloch, Ill. Nat. Hist. Surv. Bull. 13: 7, 17, 1918.

Malloch described this species from a female collected by A. H. Manee at Southern Pines, North Carolina, June 23, 1910. He does not mention other material, hence this specimen is probably the only one seen. There is a female at the Museum of Comparative Zoology with the above information and designated "type 10251." I designate it as the lectotype.

T. incisurata differs from *pennsylvanica* which also has a transverse carina on the dorsum of the first tergite, in the characters described below. The type has a narrow band of relatively coarse primary punctures on the median extension of the clypeus, and the punctures extend irregularly to its apex which has no impunctate margin. The hind basitarsus on its inner face has a very shallow, vestigial groove, scarcely one-third the length of the joint. The intermediate abdominal tergites on the apices posterior to the primary punctures, each has a close single row of minute punctures continuous over the dorsum. The side of the propodeum on lower half is shagreened with its microscopic hairs sparse and inconspicuous.

THE TACHINIDS (DIPTERA) OF TRINIDAD. I. THE VORIINES

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This paper is intended to be the first of a series dealing comprehensively with the tachinids of Trinidad. Some introductory remarks are therefore necessary.

References to tachinids collected in Trinidad are scattered through the literature. In Townsend's *Manual of Myiology* (1934–1942) some 45 species are recorded. A list of West Indian species in the British Museum collection, kindly compiled for me by Dr. W. J. Hall, comprises about 80 species, but the precise location of the specimens was not given and it is certain that many of them are not from Trinidad but from islands ecologically very different, such as Cuba and Jamaica. The collection of the Imperial College of Tropical Agriculture contains only a small number of species, though some bred but undetermined material of interest was found in it.

The fauna of Trinidad, as is well known, is closely allied to that of the South American mainland, from which it is separated only by a narrow interval of shallow water. The fauna and flora of the lesser Antilles differs in many respects from that of Trinidad. Even in the island of Tobago, which is visible on a clear day from the northern range of the larger island, there are birds not found in Trinidad.

It was originally intended to extend this study to the West Indies in general. However, the time and money required to explore the many islands in the group and the practical certainty of a very great increase in material with quite different faunistic relationships and, finally, the unexpected richness of the Trinidad tachinid fauna, made the project impracticable, at least for the present writer. The study has therefore been restricted to Trinidad. The bulk of the material was collected by Dr. F. J. Simmonds, Mr. F. D. Bennett and their assistants from 1952 to 1954

inclusive, but additional collections were made by the writer with the help of Mr. F. D. Bennett and his assistants during the winter of 1959–1960.

The collection now on hand is estimated to contain between 200 and 250 species. These have been divided rather roughly into the main taxonomic groups recognized by Professor L. P. Mesnil and empirical keys to these various sections have been prepared. These keys have been progressively modified as new material became available.

Since there is no published work dealing with the tachinids of Trinidad and the fauna has really not much in common with that of the Nearctic region, the identification of the Trinidad species has been very difficult. C. H. T. Townsend's *Manual of Myiology* and his "*Synopse dos generos Muscoideas da região humida tropical da America, com generos e especies novas*" (1927), cover a mass of genera and species which are taxonomically related to Trinidad tachinids and are in many cases identical. The difficulties in the use of these monumental works are well known, arising not only from the special character of Townsend's taxonomic concepts, but also no doubt from the isolated position he occupied during his later years. Fortunately, a great many of Townsend's types are available in the collection in the United States National Museum, but only too often, the possibility of regional variation combined with the very restricted character of Townsend's genera and species, makes identification and the choice of a name rather hazardous. When types are not available for study or have not been examined by specialists in the group, the uncertainty increases, since in some of the old descriptions the most distinctive characters may be overlooked.

Under these circumstances, the writer has considered that it is impracticable to pursue, beyond a certain point, the attempt to identify certain forms with described species or genera in a manner that admits of no doubt. He has decided also that in most cases an attempt to simplify the taxonomic problems by reducing Townsendian genera to the synonymy is impracticable because with the knowledge we now have it is impossible to know when to stop.

The method adopted by the writer has been the following: to provide empirical keys that allow the Trinidad species to be recognized on adult characters and to attach to these species the names to which they correspond as well as can be determined at this time; to reinforce the specific identity by the careful and detailed description of larval forms when these are available.

This attempt to use the larval morphology to consolidate specific identity and test the taxonomic relationships based on adult characters is the distinctive effort of this work. Originally inspired by Dr. C. H. T. Townsend, the writer has worked for a long period on the larval morphology of the tachinids and their allies, has described the larvae of more than one hundred and twenty-five species and has available for study a much greater number representing both Palaearctic and Nearctic genera. Occasionally, he has ventured to indicate the agreements or disagreements between the taxonomic arrangements based on adult characters and those suggested by larval characters. More often, he has left to the specialists who have worked with adult characters, the task of drawing the necessary deductions from larval studies and of introducing into their systems any modifications they seem to entail. This negative attitude has not proved fruitful. From time to time the striking larval differences between species supposed to be closely allied has been recognized, but not as a result of the larval studies. An excellent example is that of the old genus of green metallic Tachinids, *Gymnochaeta*. A study of the larval forms of the species in this genus (Thompson, 1923), showed that they were of two very different types, one including *alcedo* Loew and the other *viridis* Fall. and *ruficornis* Will. In 1926, J. M. Aldrich, without reference to these larval studies, subdivided the species between *Gymnochaeta* and *Chrysotachina*. The division thus separated the two types of larvae. Aldrich (1927) also referred to the differences described by the writer (1922) in several forms considered by specialists to be conspecific or only variants of *Lydella grisescens* R.–D. The importance of larval characters in the tachinids was long ago stressed by Robineau-Desvoidy. Townsend regarded them of great importance, but though he accumulated, sketchily figured and very briefly described, the larval characters of a good many forms, he

was unable to follow up this work. Some of the foremost students of the group threw doubt on the idea that reproductive habits and larval forms are taxonomically significant. The late Père Pantel. S.J., (1910) suggested that similarities in these characters are merely the result of evolutionary convergence. Aldrich and Webber (1924), in their monograph of *Phorocera,* say that the difference between the macro and micro-type eggs is of no more importance than the difference between the large and small eggs of hens. These differences, they thought, are geologically recent and therefore less significant than the adult characters, which they presumed to be ancient. To this Townsend replied that the micro-type egg habit is probably very ancient but in any case, this has little bearing on the matter. On the other hand, the introduction of the micro-type egg habit into the generic definition of *Zenillia* by W. F. Sellers (1943) via the description of the female abdomen, of which the form is correlated with this habit, makes an advance which may have far-reaching taxonomic consequences. This supports Townsend's view that the micro-type egg species probably constitute a taxonomic unit though it cannot be defined at present on adult characters. The present writer considers that if " evolutionary convergence " has occurred—a matter on which, in fact, we have no information—it can have occurred as easily in relation to adult as in relation to larval characters. To the worker who has really acquired a knowledge of tachinid larvae, the morphological patterns they present very often stand out in the most marked contrast, to the permutations and combinations of adult characters on which the genera are usually based. To describe the difference between the macro- and micro-type egg species as of the same order as that between hens with large and hens with small eggs is a great mistake. Between the two Tachinid types there is a vast difference in a whole series of correlated characters in the eggs, the larvae and the adults.

The systematic recognition of larval characters in taxonomic work is an innovation that can hardly be welcome to most workers since it greatly complicates their tasks. In very many species of the Tachinidae (s. lat.), larvae can be extracted from the female fly, but there are others (e.g. *Exorista, Phorocera,*

Winthemia, Nemorilla, many phasiines) which deposit undeveloped eggs. The removal and preparation of the eggs or larvae is a rather laborious and delicate operation, even with fresh material and dry material seldom emerges uninjured from the process. There is therefore a natural and justified reluctance to attempt it with rare species and types. Furthermore, the larval characters require special study and their systematic description is often difficult. The primary larval characters frequently indicate taxonomic affinities, but sometimes the characters of the later stages give important additional clues. For these various reasons, the introduction of the knowledge of larval forms into a system based on adult characters must naturally be difficult and hesitating, but the results so far obtained have convinced the writer that it will be worth-while. In these papers therefore an attempt will be made to draw all the taxonomic conclusions that seem justified by the comparison of larval forms in relation to the classifications based on adult characters.

Since this paper and those which will follow it are planned as a monograph of the Trinidad tachinids, it might appear desirable to begin with a definition of the group treated and a subdivision into its recognized sections. However, readily accessible text-books and monographs define the Tachinidae, readily recognized by their hypopleural bristles, well developed postscutellum, 1st posterior cell narrowed or closed in the wing margin. On the contrary, the subdivisions, though easily recognizable in certain characteristic or " typical " elements, are difficult to define clearly and simply. For example, the " dexiines " are usually described as flies with long legs, plumose arista, cheeks broader than the length of the 2nd and 3rd antennal joints together, and a distinct facial carina. The presence of a single genital paramere attached to the base of the aedeagus is also regarded as distinctive. But the last named character has not as yet been verified in all the forms considered on other grounds to be dexiine, while many that are so considered positively do not correspond in all respects to the definition. Similar difficulties occur with the other main subdivisions and with the lower categories, as they are defined by authorities such as Mesnil or Van Emden, they become more acute. An attempt to apply

their "keys" to the Trinidad material would not be very illuminating.

It has been decided that the only practical procedure is to follow in a general way the taxonomic order recognized by specialists, but to deal successively with such groups as can be precisely defined in terms of the characters they really present. Sometimes the group will include a number of genera of which the species cannot be treated in a single paper. More restricted groups can be dealt with *in toto*. Such is the first group selected: a group comprising only three genera, each with a single species —the voriines. Most systematists regard the voriines as a taxonomic unit, characterized mainly by the retracted hind cross-vein and the long coiled phallus of the male. But certain genera (e.g. *Minthomima*) having the second character have not the first, and Townsend suggests that the second may not hold good in all the forms he places in his "voriines". The definition given above excludes *Minthomima* but circumscribes a group that is, at least easily recognizable from the characters given and seems also from the larval characters to be taxonomically homogeneous.

Characters of the Voriines.—Prosternum bare; hind cross-vein retracted, very oblique, even more so than the apical cross-vein; R_{4+5} bristled to or beyond small cross-vein; a strong stub at bend of medial vein; apparent sub-apical scutellar bristles strong, widely separated, as far from apex as from base of scutellum, apical bristles strong and cruciate; front very broad in both sexes, male with orbital bristles; no black setulae behind the upper half of the occipital row; infrasquamal setulae present; no postero-ventral spine at end of hind tibia.

Three species of this group were obtained in the Trinidad collections: *Eucyrtophloeba horrida* G.T., *Minthoplagia rafaeli* T.T., *Voria ruralis* Fall.

Key to the Trinidad Voriines

1. No proclinate bristles below lowest frontal; R_1, R_{4+5} and Cu_1 bristled; eyes hairy; ocellar bristles divaricate, inserted in front of anterior ocellus; 2nd abdominal tergite not excavated to posterior margin; one row of strong bristles on tergite V, the dorsal pair set forward *Minthoplagia rafaeli* T.T.

One or more strong proclinate bristles below lowest frontal; Cu_1 bare; ocellar bristles inserted on or behind line of anterior ocellus; 2nd abdominal tergite excavated to posterior margin; two rows of bristles on tergite V, the bristles of each row in line 2

2. One proclinate bristle below lowest frontal; R_1 bristled to tip; R_{4+5} to small cross-vein; eyes bare; ocellar bristles weak, divaricate, inserted on or behind line of anterior ocellus ..... *Voria ruralis* Fall.

Four or five proclinate bristles below lowest frontal; R_1 bristled to point opposite bend of subcosta; R_{4+5} bristled to point opposite hind cross-vein; eyes hairy; ocellar bristles weak, proclinate, inserted behind line of anterior ocellus ..... *Eucyrtophloeba horrida* G.T.

Minthoplagia rafaeli T. T.

Minthoplagia rafaeli T.T.; Townsend, Ins. Insc. Menst. III: 92, 1915.

Head about 1.4 times as wide as high in front view; head at base of antenna 2 times width of eye at same level; cheek about $\frac{1}{9}$ eye height; clypeus sunken; parafacials at base of antennae about 2.5 times as wide as facials at widest point; occiput almost flat; no occipital extension; proboscis short, palpi yellow, about as long as proboscis, slightly clavate; antennae inserted at point above middle of eye height, 1st joint rather elongate, about $\frac{1}{2}$ the length of 2nd, these 2 joints and base of 3d yellowish-red, the 3d joint about 2 times length of 2nd, brown except at base; arista thickened only on about basal $\frac{1}{4}$th, pubescent, brown, the basal joints short; vertical bristles strong, equal, the inner bristles cruciate, in front of the verticals, a reclinate bristle, directed obliquely outward, in front of this, 3 strong proclinate orbitals; along the inner edge of parafrontals, 5 or 6 strong bristles, the posterior bristle reclinate, much the strongest, lowest frontal below the base of 3d antennal joint; a few fine scattered hairs on the parafrontals, the parafacials bare below the frontals; ocellar bristles moderately strong, divaricate, inserted in front of the level of the anterior ocellus; vibrissae inserted opposite middle of oral margin, one moderate bristle above the vibrissae, a row of strong bristles extending along the lower edge of the cheek and blending with the occipital row; behind the junction a few strong bristles near the oral margin; propleura bare; acrostichals 3 : 3, the posterior presuturals near the suture, dorsocentrals 3 : 3; intra-alars 1 : 2; post-sutural supra-alars 3, the anterior and posterior weak, the middle one very strong; humeral bristles 4, the posterior 3 in a line, the 4th opposite the space between the inner and the median bristle; sternopleurals 3; pteropleurals weak; several infrasquamal setulae; 3 marginal and strong cruciate apical scutellars, the second marginals (the apparent sub-apicals) very strong, extending to the base of segment IV, widely separated at the base, the true sub-apicals weak; discals not very distinct from the other dorsal scutellar hairs. Abdomen slightly compressed laterally, about 1.4 times the length of the thorax including the scutellum; 2nd tergite not excavated to the posterior margin which bends markedly forward toward the middle; margins of the following tergites straight; segment II without discals or marginals; III with a pair of strong erect

marginals, set forward but no discals; segments IV and V each with a marginal row but no discals, the dorsal pair on V set forward, the bristles strong, sub-erect, the abdominal hairs depressed; wings yellowish toward costa, R_1 bristled to tip, R_{4+5} almost to the level of the end of R_{2+3}; Cu_1 to a point near the level of the small cross-vein; apical cell broadly open far before wing-tip; apical cross-vein markedly concave toward its junction with M_3, with a marked brown stub slightly longer than the small cross-vein; hind cross-vein with the anterior end about $\frac{2}{3}$ the distance from the small cross-vein to the bend, its posterior end retracted, the last section of Cu_1 more than half the length of the preceding section; legs rather stout, 1 strong posterior bristle on tibia I, several anterior bristles on tibiae II and III, 2 strong dorsal terminal bristles with a weaker one between them on tibia III, also 2 terminal ventral bristles; claws and pulvilli of male tarsi I and II elongate, those of III short; of female short on all tarsi.

Head, except the frontal vitta, silvery pollinose, the ocellar triangle slightly shining; thorax thinly silvery pollinose with broad outer and narrow inner vittae before the suture, less distinct behind it; abdomen black, shining with anterior silvery bands, the first, on segment III, emarginate behind, occupying about the anterior fourth of the segment; bands of segments IV and V slightly broader, only slightly emarginate in the middle; legs dark brown but the anterior femora silvered on the posterior side. (Fig. 13) (8–10 mm.).

Voria ruralis Fall.

Voria ruralis Fallen, Vet. Akad. Handl. XXXI: 265–266, 1810; Fallen, Dipt. Suec. Musc., 5–6 (*Tachina*), 1820. Syn. *americana* van der Wulp, Biologia, Dipt. II: 102, pl. III, fig. 19, 1890; ?*mexicana* Giglio-Tos, Boll. R. Univ. Torino, no. 158, 1893; Ditt. del Mess. III: 42, fig. 13; *brasiliana* Townsend, Rev. Chil. Hist. Nat. 32: 380, 1929.

Head about 1.3 times as wide as high in front view; head at base of antenna 3.5 times width of eye at same level; cheek between $\frac{1}{5}$ and $\frac{1}{6}$ eye height; clypeus only slightly sunken, practically on same plane as parafacials; parafacials at base of antennae about 2 times as wide as facials at widest point; occiput slightly convex below; no occipital extension; oral margin moderately protruding; proboscis short, palpi about as long as haustellum plus labella, brown on basal half, yellow on apical half, slightly clavate; antennae inserted slightly above level of eye middle, 1st joint short, about $\frac{1}{2}$ the length of 2nd, tip of 2nd joint reddish, remainder brown, length of 3d joint about 1.5 times length of 2nd joint, 3d joint enlarging distally, broadly rounded at end; arista bare, only slightly exceeding length of 3d antennal joint, thickened on basal $\frac{1}{2}$, brown, the basal joints short; vertical bristles strong, equal, the inner bristles erect, parallel, in front of the verticals, a minute outwardly directed bristle, then 2 reclinate bristles, then 3 strong inwardly directed bristles and between the 1st and 2nd, 1 or 2

finer bristles, the row descending to a point slightly below the level of the middle of the 2nd antennal joint; below the lowest bristle of the row, a single strong proclinate bristle, numerous fine pale hairs on the parafrontals and upper half of parafacials; outside the parafrontals, 3 proclinate orbital bristles all usually strong but one sometimes weaker; ocellar bristles rather weak, divaricate, inserted opposite or slightly behind middle of anterior ocellus; numerous fine pale hairs on ocellar triangle; vibrissae strong, cruciate, inserted opposite level of oral margin, above the vibrissa a few weaker bristles, facials otherwise bare; a row of strong bristles along oral margin; propleura bare; acrostichals 3 : 3, the posterior presutural pair close to the suture; dorsocentrals 3 : 3; intra-alars 3 : 3; post-sutural supra-alars 3, the anterior bristle very short, the middle one very strong; humerals 4, the 3 posterior bristles in a line, the 4th opposite the space between the inner and median bristle; sternopleurals 3; pteropleurals very weak; 7 or 8 infra-squamal setulae; 2 strong marginal and strong cruciate apical scutellars, 1 or 2 additional weaker bristles, between 1st and 2nd marginals and between marginals and apicals; the apparent sub-apicals which are the strongest, widely separated, less than ½ way from base to apex of scutellum; 1 or 2 pairs of rather short sub-erect discal bristles opposite the interval between the cruciate apicals, one pair behind the other; abdomen oval in outline, seen from behind, not compressed laterally, about 1.3 times the length of the thorax, including scutellum; 1st segment excavated to posterior margin; margins of all segments straight; segment II without bristles; segment III with a pair of marginals set slightly forward; segment IV with a row of marginals; segment V with a row of marginals and a row of discals; the bristles moderately strong, reclinate, the abdominal hairs depressed; wings slightly yellowish above R_{2+3}, otherwise colourless; costal spine weak; R_1 bristled to tip; R_{4+5} bristled to a point beyond small cross-vein and about opposite the lower end of hind cross-vein; Cu_1 bare; hind cross-vein with the anterior end about halfway from small cross-vein to bend of M_1, posterior end retracted, the last section of Cu_1 about ⅔ length of preceding section; apical cell rather broadly open far from wing-tip, apical cross-vein markedly concave below, meeting M_1 at right angles, a marked stub at the bend; Cu_2 bends downward toward its end; legs rather stout, 1 strong and above it, 1 weaker bristle on tibia I; several dorso-anterior bristles and 2 dorso-posterior bristles on tibias II and III, 2 strong terminal lateral bristles, 1 strong ventral between two weak bristles on tibia III; claws and pulvilli moderately elongate on all tarsi in male, shorter in female.

Head except the frontal vitta, rather densely pollinose, slightly shining toward occiput, faintly brassy on para-frontals and para-facials, elsewhere silvery; thorax black, thinly pollinose, with 2 broad outer and 2 narrower inner vittae before the suture; scutellum black, thinly pollinose; abdomen seen from behind, black, thinly pollinose near anterior margin of segment III, on anterior half of segment IV and anterior third of segment V; legs black, inner side of femora I faintly silvery. (Fig. 2) (7–9 mm.).

Eucyrtophloeba horrida G.–T.

Eucyrtophloeba horrida Giglio-Tos, Boll. R. Univ. Torino VIII, no. 158, 1893; Ditt. del Mess. III: 40, f. II (*Cyrtophloeba horrida*), 1893. Syn. *rhois* Townsend, Proc. U. S. Nat. Mus. 51, no. 2152: 316 (*Eucyrtophloeba rhois*), 1916.

Head about 1.45 times as wide as high, in front view; head at base of antenna about 3.0 times width of eye at same level; cheek between $\frac{1}{5}$ and $\frac{1}{6}$ eye height; clypeus slightly sunken, gently curving into facials; parafacials at base of antennae about 1.5 times as wide as facials at widest point; occiput flat; no occipital extension; oral margin very slightly produced; proboscis short, palpi about as long as haustellum plus labella; slightly clavate, yellow to base; antennae inserted slightly above level of eye middle, 1st joint short, about $\frac{1}{3}$ length of 2nd joint, 3d joint about 2 times the length of 2nd; 1st joint brown reddish on front edge; 2nd joint bright red, contrasting with 3d which is brown except for a narrow margin at base; 3d joint rounded at end; arista brown, slightly pubescent, thickened on basal third, basal joints short; vertical bristles strong, the inner verticals erect, parallel, the outer about $\frac{3}{4}$ the length of the inner, directed obliquely outward; in front of the verticals a strong outwardly directed bristle; in front of this, 3 strong proclinate orbitals, 1 or 2 weaker inwardly directed bristles, below these a row of 4 or 5 proclinate parafacial bristles extending to a point slightly above the upper facial hairs; along the frontal vitta 3 more or less reclinate strong bristles continued by a row of frontals of which the upper 3 cross those of the opposite side, while the 4th, which is opposite the end of the 2nd antennal joint, is directed forward and upward; parafrontals and parafacials also bearing sparse fine black hairs, which are numerous also on the ocellar triangle; ocellar bristles moderately strong, proclinate, inserted slightly behind the level of the anterior ocellus; vibrissae strong, cruciate, inserted on a level with the oral margin, only 2 or 3 weak bristles above them; below the vibrissae, several rather strong bristles along the oral margin, an isolated bristle on the edge of the occiput about $\frac{1}{3}$ the way from the eye to the oral margin; propleura bare; acrostichals 3 : 3; the posterior presuturals close to the suture; dorso-centrals 3 : 3 or 3 : 4, but the row behind the suture usually "spaced for 4" with a gap between the 1st 2; intra-alars 2 :3; post-sutural supra-alars 3, the anterior very weak, the 2nd long and strong; humerals 4, the posterior 3 in an oblique line, the 4th opposite and in front of the space between the median and the inner; sternopleurals 3; pteropleurals very weak; a few infrasquamal setulae; 2 strong marginal and 2 strong cruciate apical scutellars, some weaker bristles in the intervals, the apparent subapicals widely separated, about half way between base and apex of scutellum; opposite the interval between the apicals and near the tip of the scutellum a pair of strong erect discals, behind which are two similar but weaker pairs; 1st abdominal segment excavated to posterior margin; margins of all segments

straight; segment II without bristles; segment III with a pair of strong erect marginals, set slightly forward; segment IV with a row of strong marginals; segment V with a rather irregular row of strong discals and a row of weaker marginals; abdominal hairs depressed; wings slightly smoky toward costal margin; costal spine weak; R_1 bristled to bend to subcosta; R_{4+5} bristled to a point about opposite lower end of hind cross-vein; Cu_1 bare; hind cross-vein with the anterior end distinctly more than half way from small cross-vein to angle of M_1, posterior end retracted, the last section of Cu_1 about $\frac{5}{7}$ the preceding section; apical cell open far before wing tip, a long stub at the angle of M_1; legs rather stout, bristly; hind coxae bare; tibiae I with 2 posterior bristles, the upper one weaker; tibiae II with 5 or 6 rather strong dorso-anterior bristles and 2 dorso-posterior bristles; tibiae III with a similar row of dorso-anterior bristles and 3 dorso-posterior bristles; 3 dorsal terminal bristles and 2 ventral terminal bristles; claws and pulvilli all short in female; in male claws of anterior and middle tarsi long, of posterior tarsi short.

Head thinly greyish pollinose; thorax black, faintly greyish pollinose with faint anterior vittae, the outer broader than the inner; vittae indistinct behind the suture; scutellum thinly grey pollinose; abdomen black with well-marked anterior silver bands, covering about $\frac{1}{4}$ the length of segments III and IV and $\frac{1}{3}$ of segment V; legs black. Smaller than the two preceding species, on the average. (Fig. 6) (5–8 mm.).

Minthoplagia rafaeli T.T. was compared with the type in Washington. The Trinidad *Voria* seems to be the same as the species described by van der Wulp as *americana* and by Townsend as *brasiliana* but does not differ from a specimen determined by Villeneuve as *ruralis*. This was also the view of Aldrich. The *Eucyrtophloeba* runs in the *Manual of Myiology* to *rhois* T.T. Aldrich considered *rhois* to be a synonym of *horrida* G.T. Townsend says in the *Manual of Myiology* (Vol. VIII, p. 380) that *horrida* G.T. is distinct from *rhois* but gives no grounds for the statement. I have accepted the view of Aldrich.

The Larvae of the Voriines

My larval material of the voriines which includes both Palaearctic and Nearctic forms, indicates a great distinctive uniformity in the primary larvae with a considerable divergence in stages II and III.

The species described by Townsend and van der Wulp as *brasiliana* and *americana* were regarded by Villeneuve and Aldrich as indistinguishable from *ruralis* Fall. I cannot separate

the stage I larvae of this species and the description and figures of the puparium of *Voria americana* given by Greene correspond perfectly to the puparia of *ruralis* in my collection, reared in Europe, therefore, I have no reason to regard the Trinidad species as distinct from *ruralis* Fall. I am therefore completing the account of the larval forms by adding the descriptions of the stage II and III characters of the European *ruralis* from specimens reared by the late M. P. Chrétien from *Deiliphila euphorbiae* (20. vii–13 viii, 1914), in France. I have been able only to obtain of stage II, the buccopharyngeal armature, the posterior spiracles and " felt-chambers " and a small piece of the cuticle and of stage III, such characters as may be seen in the puparium. However, unless the Trinidad species differs in stages II and III from the European *ruralis*, these features, which are very characteristic should easily allow its identification if it is found by dissection in a Trinidad host.

Voria ruralis Fall.

Stage I: Length, 0.499 mm., width, 0.185 mm. Head without spines, the antennae small but elongate, about 3 times as long as wide at the base; segment I with an anterior band of 3 to 4 rows of minute but dark spines; segment II with a similar but broader anterior band with as many as 10 or 11 rows on the dorsum and 4 rows on the venter; segments III and IV bare; segments V to X with small ventral median patches of small spines, 6 spines wide and 2 rows deep on V and VI, about the same width but 3 or 4 rows deep on VII to X; opposite these, on the dorsum, along the conjunctivae of VI–VII to X–XI inclusive, bands of 1 or 2 rows of short spines, the pleural areas bare; segment XI with a band of 3 or 4 rows ringing the spiracular area; spiracles (Fig. 3) small, each with 2 respiratory papillae; felt-chambers very slender, 1. about 0.026 mm., about 10 times as long as wide.

Buccopharyngeal armature (length, 0.090 mm.) (Fig. 1), pale brown, the anterior region (or labial sclerite) roughly quadrate, the apex well above the middle of a dorso-ventral line crossing the base, the three angles gently rounded, the upper angle above the dorsal edge of the intermediate region; dorso-anterior border with irregular pale narrow stripes; the ventro-anterior border with close fine regular striation and a finely serrated edge, the striations forming a dark band which continues around the ventral angle toward the base; anterior and intermediate regions together about 1.75 times the dorsal wing of the posterior region measured from the anterior end of the inter-alar space to the tip of the dorsal wing; intermediate region at its narrowest part little more than ¼ the height of the anterior region; dorsal

wing of the posterior region clavate, markedly longer than the ventral wing; inter-alar space acute in front; lateral anterior sclerites ribbon-shaped, apparently joining across the roof of the mouth; sclerite of the salivary gland well developed.

During stage I, the pigmentation of the pharyngeal wall develops as a narrow oblong extension of the end of the dorsal wing, which at the end of the stage is somewhat larger than the original dorsal wing.

Stage II.—The cuticle, in the anterior region at least, bears some bands of small acute spines; the buccopharyngeal armature (length, 0.285 mm.) (Fig. 4) is of an extremely unusual type which cannot be easily interpreted morphologically without sections for which material is not now available. The first specimen found was thought perhaps to be abnormal, but as a second specimen was essentially the same, the form must be characteristic of this species. The posterior region is normal with the usual dorsal and ventral wings; the intermediate region is reduced to a mere bridge behind the anterior region and this consists of a short hollow cylinder, whose outline roughly resembles that of the anterior region in stage I, and may be regarded as the homologue of the paired mandibular hooks, fused dorsally and ventrally into a short tube with an irregular anterior edge, quite unlike the outline of the normal anterior hook. The organ appears to function like a scoop. The posterior spiracles (Fig. 3) are well developed, each with a pair of respiratory papillae, the felt-chambers short and stout (length, 0.12 mm.), markedly enlarged on their inner $\frac{3}{4}$.

Stage III.—The buccopharyngeal armature (Fig. 12) (length from tip of anterior hook to tip of ventral wing, 0.7 mm.) presents large posterior wings markedly divergent as in stages I and II, a very short intermediate region and rather irregular short anterior hooks at the base of which is a short stout ventral process; the sclerite of the salivary gland is normal and behind it is the hypopharyngeal sclerite. The presence of the paired hooks in this stage might suggest that they were present also in stage II and became detached during the moult since they were not present on the specimens when they were found in the host caterpillar. Since the various regions of the stage III armature are solidly fused together, it is hardly likely that they would be loosely articulated in stage II. The puparium (length, 6.5 mm.; width, 4 mm.) (Fig. 14) is somewhat egg-shaped, slightly enlarged posteriorly, surface dull. Anterior spiracles (length, about 0.4 mm.) separated, prominent, black, cylindrical at base, apically definitely flattened, with a row of 10 or 12 respiratory papillae across the top, the row doubled at the ends; the basal half of the spiracular horn is set with very short scattered points. Posterior spiracles (Fig. 11) prominent, black, dorsad, set well back from the posterior extremity, directed dorso-caudally, in the form of half-cylinders, with the flat sides inward, separated at their bases by a narrow line, the sides set with small points, each spiracle bearing 4 more or less curved spiracular slits, a deep depression between the 2 pairs: anal opening nearer the longitudinal lateral axis than the base of the spiracles.

My specimens of the puparia of *Voria ruralis* do not agree with the description given by Greene who says that each spiracular plate has 3 small slits. They agree with the figure given by H. L. Parker (1953), whose figure of the stage I buccopharyngeal armature also agrees reasonably well and shows the characteristic extension of the dorsal pharyngeal wing at the end of the first stage. Since Parker's material was South American, the argument that the species is *Voria ruralis* Fall., is strengthened.

It is difficult to determine the distribution of spines in the puparium because the pigmentation eliminates the contrast between the spine bands and the cuticle. These bands can usually be seen on some part of the puparium and I have not detected them in *Voria ruralis*.

In *Voria ruralis* the prepupal prothoracic spiracles are present, composed of the usual branching respiratory arms bearing numerous papillae, but the respiratory cornicles are absent.

Eucyrtophloeba horrida G.T.

Stage I: Length, 0.37 mm.; width, 0.11 mm. Head without spines, antennal organ short-oval; segment I with an anterior spine band of 3 or 4 rows of small black elements, the band narrowing in the pleural areas; segment II with a similar anterior band, of 1 or 2 rows dorsally, broadening to 7 or 8 rows pleurally, interrupted ventrally; segment III with 2 short dorso-pleural patches of 2 or 3 rows, connected by rows of extremely pale spines; on the conjunctivae of segments V–VI to IX–X, 5 rather short dorsal bands of 1 or 2 rows; on the conjunctivae of VII–VIII to X–XI, a short pleural patch on each side; a few scattered black and numerous, almost colorless, spines on the area around the posterior spiracles; spiracles small, each with 2 respiratory papillae, the felt-chambers short (length, 0.027 mm.), about 5 times as long as wide.

Buccopharyngeal armature (length, 0.066 mm.) (Fig. 24) much smaller than that of *Voria ruralis* but very similar in form, the dorsal angle of the anterior region more prominent, acute, the pale striping on the dorso-anterior border present, the ventro-anterior edge with a narrow pale border, and with some very minute serrations but without obvious striations; ventral angle rounded, the other differences shown in the figures.

This larva closely resembles that of *Cyrtophloeba coquilletti* Ald., but in my only specimen of the latter there are 5 small ventral spine patches on the conjunctivae of V–VI to IX–X. I do not find these in *E. horrida* G.T. Furthermore, the abdominal pleural spine patches, in *coquilletti*, are only on VIII–IX, IX–X and X–XI.

Minthoplagia rafaeli T.T.

Stage I: Length, 0.528 mm.; width, 0.15 mm. The larva is notably larger and more robust than those of the two other species treated here. The head bears a notably elongate cylindrical antenna, rounded at the end; segment I with a rather strong anterior spine band of 4 or 5 rows, expanding below the mouth into a broad rounded patch of 9 or 10 rows of fine rather elongate elements; segment II with a similar band of 3 or 4 rows dorsally, broadening to 7 or 8 rows pleurally, diminishing again to about 3 rows ventrally; segment III with a few scattered spines across the anterior dorsal border, 3 pleural patches on each side, with about 15 spines each, the dorsal patch separated from the others which touch at their inner borders; ventrally a band of 2 or 3 rows, separated from the pleural patch at each end; dorsal area of IV to VIII inclusive, bare; segment IX with an anterior dorsal band and a narrower posterior dorsal band, ventrad of which are scattered spines, at the end of which is a remarkable group of spines consisting of one very large elongate triangular element, 2 very small elements and 3 of intermediate size (Fig. 7); above this group a rather prominent rod-shaped sensorial organ; segment X with a dorsal anterior band of 4 or 5 rows, and a posterior band of 3 or 4 rows at each end of which is another group of the large spines, one very large, 2 much smaller; segment XI appears to be spineless; but on the ventral side of segments IV to IX is a pair of spine patches, each of some 20 fine elements; the last two pairs tend to fuse in the mid-ventral line. The posterior spiracles have each two respiratory papillae; the felt-chambers are elongate (length, 0.054 mm.), about 7 times as long as wide.

Buccopharyngeal armature (length, 0.12 mm.) (Fig. 5) of the same general type as the other voriines, but larger and stouter; anterior region quadrate, with the characteristic voriine striping, particularly on the antero-dorsal edge; dorsal angle tooth-shaped, acute, anterior angle less so, ventral angle rounded; ventro-anterior edge very finely serrated, with a dark marginal strip in which indistinct striations are visible; intermediate region rather short and stout, its length from the base of the anterior sclerite to the base of the ventral wing little more than 0.5 the length of the anterior sclerite from base to tip; dorsal wing of the posterior region markedly clavate, diverging strongly from the ventral wing; sclerite of the salivary gland well developed; each of the anterior lateral sclerites (corresponding to the stage II and III mandibles) appear in this species to be fused with the opposite sclerite in such a way as to form pigmented dorsal and ventral arches or cups, lining the opening of the mouth.

The larva described above from specimens collected in Trinidad, is inseparable from a larva dissected by C. H. T. Townsend, obtained from his T. D. larval collection in the U. S. National Museum, Washington.

Biology

Nothing definite is known at present about the biology of the Trinidad voriines discussed in this paper. There is, however, some information about the larvae, reproductive systems, oviposition and larval biology of other voriines. J. Pantel (1910) studied the female reproductive system of *Cyrtophloeba ruricola* Meig. under the name of *Cyrtophlebia ruricola,* of *Steinomyia elata* Meig. under the name of *Cyrtophlebia elata,* of *Voria ruralis* Fall., under the name of *Plagia ruralis* and *Athrycia trepida* Meig. under the name of *Paraplagia trepida.* F. Silvestri (1911) gave some data on the stage III larva of *Voria ruralis* and figures of the skin of the host caterpillar (*Plusia gamma* L.) containing puparia in their characteristic position. Finally, in 1915 I gave brief descriptions of some of the larval stages of the European *Voria ruralis* Fall., the North American *ruralis* (under the synonym of *Plagia americana*) and *Cyrtophloeba coquilletti* Aldr., under the name of *C. horrida* Coq., and described the larval biology of *Athrycia trepida.*

As shown by Pantel, the species he examined fall into his reproductive group VI. The reproductive capacity is moderate, the ovaries have the form of two rather voluminous packets of ovarioles which usually become empty as the eggs descend, and are therefore not replaced by new oocytes from the terminal chamber. The number of ovarioles varies and may reach 54 in *Steinomyia elata.* In each ovariole there are 6 or 7 chambers and 3 short-pedicelled spermathecae with a geniculate pedicel. The spermathecae are usually pigmented, but hyaline in *trepida.* The accessory glands are relatively short. The posterior uterus is an incubating organ, rather short at emergence, elongating as it fills with eggs, which are irregularly arranged in *trepida.* There is no piercing organ. The egg is thin shelled, varying in length, according to Pantel, from 867μ in *trepida* to 460μ in *ruralis,* though my specimens of stage I larvae removed from females flies are of practically the same size. The chorion shows the usual fine stippling and, says Pantel, the ordinary polygonal network though the latter is sometimes very indistinct. Herting (1957) says that the egg-shell has a broad white band, but no white reticulum. In my specimens of *Voria ruralis* both from

Europe and America, the reticulum is, however, exceptionally obvious. The micropyle has the form of a mucous stopper, expanding in *ruralis* and amorphous in *trepida*. Pantel also refers to a pneumatic apparatus and this appears to be the girdle referred to by Herting.

Pantel made some reproduction experiments with *ruricola*. He did not observe oviposition but eventually found numerous eggs on the body of the host (*Spintherops spectrum*), and from one of these a larva had hatched and entered. In further observations he found that the larva of *ruricola* enters a cutaneous muscle fiber and after leaving this, makes an opening in the host cuticle from which an integumental sheath develops. It does not seriously injure the host in the early stages but later begins feeding more actively and destroys all the organs in its vicinity. In *ruricola* it remains in the integumental sheath until it is ready to pupate.

Silvestri found that *Voria ruralis* pupates in the host skin and my European material resembles his figures. However, I found that the larva of *trepida* emerges from the host. The habits of this species correspond to those of *ruricola*. I found, however, that the pathological changes produced in the muscle fiber (Fig. 8) were not, as Pantel seemed to suggest, like those produced by such species as *Sturmia bella* Meig. (studied by Pantel under the name of *S. pupiphaga* Rdi.) and *Blepharipoda scutellata* R.D. (studied by Pantel and the present writer under the name of *Sturmia scutellata* Rdi.) The sturmias produce an extraordinary pathological hypertrophy of the muscle fiber but the voriines merely destroy the sarcolemma. When they issue from it they leave a nearly empty sack containing only leucocytes and debris, but the *Sturmia* larva does not seem to utilise the " gall " in which it lives and apparently subsists on liquid, leaving the hypertrophied muscle intact when it issues.

In his 1915 paper, the writer gave a general account of the larval forms of the voriines studied. He noted that the primary larvae were all of the same characteristic type and this has been confirmed by further studies. One peculiarity that exists in several of these larvae, is the presence of a rectal vesicle (Fig. 19) which when devaginated, has the form of a large plate surrounding the anal opening. Pantel has suggested that this has a

respiratory function and it may be noted that the larvae living in the muscle fiber have greatly reduced spiracles and felt-chambers and have of course no direct access to the oxygen of the air.

The larvae of the later stages seem to differ much more markedly than the primary larvae as may be seen by comparing the descriptions and figures of *V. ruralis* with those of *A. trepida* (cf. Thompson, 1915). H. L. Parker (1953) has suggested that the buccopharyngeal armature of the second and third stage larvae of dipterous parasites are of very little interest. "These organs", he says, "are so much alike between species of the same genus that in most species they have no taxonomic significance". However, in a group where the status of genera is as uncertain as it is in the tachinids, the similarity noted by Parker is itself of real significance. Furthermore, marked differences between species regarded as close allies often exist. Of this, the later stages of the voriines give a striking example. The resemblance between the puparia of *Voria ruralis* and *V. americana* goes far to confirm the views reached by the study of the adults. The distinction between the stage II and III larvae of *ruralis* and *trepida* also opens up an interesting line of research.

The adult of *trepida* differs from those of *ruralis* and *ruricola* in possessing a very large pteropleural bristle whereas in the others only a few weak pteropleural hairs exist. Puparia I believe to be of *ruricola* differ from those of both *ruralis* and *trepida* though they are more similar to the former. On the whole, therefore, so far as our information goes, the separation on the pteropleural bristle, rather agrees with the separation in the late larval stages. In any case, *ruricola* differs quite markedly in adult characters from *ruralis*.

Hosts

The voriines described in this paper have not been reared in Trinidad. The North American and European species have been reared from a number of Lepidoptera and occasionally from sawfly larvae. The host lists may be found in the Parasite Catalogue of the Commonwealth Institute of Biological Control and in other standard works of reference.

Taxonomic Relationships of the Voriines

The group of the "voriines" as constituted by Townsend in the Manual of Myiology, comprises over 30 genera. In the key to the family Tachinidae, in which he places it, the tribe runs out in three places. The family itself runs out in 16 places in the super-family Oestroidea. It is therefore evident that Townsend could not define the voriines since a good definition applies to all the members of the category defined and to them alone. Townsend does mention the coiled, elongate phallus as a voriine character but surmises that it may not be present in all the genera of the group. The retracted hind cross-vein, characteristic of all the genera considered in the present paper, does not exist in all of Townsend's voriines and Aldrich (1926) showed that taxonomically unrelated forms possess it. Since I cannot see on what basis Townsend constituted his tribe of the voriines, I cannot discuss it further.

The voriines, as envisaged by L. P. Mesnil (1939) form a section of his "Larvaevorinae" or Echinomyiinae, which usually have a bare prosternum and the second abdominal segment excavated to the posterior border. Mesnil notes that *Athrycia elata* F. and *Uclesia fumipennis* Girsch., have the second segment not excavated to the posterior margin (like *Minthoplagia*) and have also a bristly prosternum.

In the work cited, Mesnil divides the voriines (or athryciines) into two groups. The first group contains *Athrycia* R.D. = *Paraplagia* B.B. (*erythrocera* R.D.), *Voria* R.D., *Plagia* Meig. and *Cyrtophloeba* Rond. which are regarded as subgenera. Here belong also *Neuroplagia* T.T., *Steinomyia* T.T., *Klugia* R.D., *Chaetovoria* Vill., *Nanoplagia* Vill., *Hypovoria* Girsch. The second group contains *Wagneria* R.D., *Phorichaeta* Rond., *Ramonda* R.D. (= *Petinops* B.B.) and *Kirbya* R.D. (*moerens* Meig.). Mesnil suggests that *Wagneria* is taxonomically related to *Petina* Meig., which, however, he places in the Macquartiini.

A study of the larval forms of the voriines and wagneriines has revealed some interesting facts which seem worth recording here, though it is necessary to refer to species not found, so far, in Trinidad.

I have examined the primary larva of *Athrycia trepida* Meig., *Cyrtophloeba ruricola* Meig., *Cyrtophloeba coquilletti* Ald., *Eucyrtophloeba horrida* G.T., *Klugia marginata* Meig. (det. by Bezzi), *Minthoplagia rafaeli* T.T. and *Voria ruralis* Fall. All of these species have, in the first larval stage, the characteristic buccopharyngeal armature with the markedly quadrate anterior region presenting near its borders the peculiar striping shown in the figures. The "felt-chambers" are usually very slender, a condition that appears to be correlated with life in the interior of a muscle fibre of the host caterpillar during the first stage. *Klugia* and *Minthoplagia*, however, show larger felt-chambers and may be in direct relation with the external air. The cuticle bears bands of spines, but no plates. The antenna is usually cylindrical, not flattened.

Between the later stages of some of these forms, marked differences exist as will be evident from a comparison of the figures and descriptions of *Voria ruralis* and *Athrycia trepida*.[1] The larval habits of *A. trepida* and *C. ruricola* seem, however, to be similar.

In the group of the wagneriines, I have seen the primary larvae of *Wagneria prunaria* Meig. (det. by Villeneuve as *carbonaria* Meig. "sec. type."), *spathulata* Fall. (det. as *lentis* Meig. by Wainwright), *succincta* Meig. (det. by Mesnil), *Kirbya moerens* Meig. (det. by Villeneuve) all from Europe and of a species doubtfully determined as *sequax* Will. (= *Wagneria helymus* Walk. according to Townsend) from North America. In the Manual of Myiology (Vol. xii, fig. 374) Townsend figures the buccopharyngeal armature of *Phorichaeta atra* Coq. referred by him to the Eriothrixini.

The larvae of *Wagneria prunaria, spathulata* and *sequax* Will. (or *helymus* Walk. according to Townsend) are all of the same type, which is quite different from that found in the voriines. The buccopharyngeal armature (Fig. 23) has the anterior region in the form of a straight elongate acute tooth, bent slightly downward at its base, near the junction with the intermediate

[1] The species referred to by me in C. R. Soc. Biol., 1915, was first determined as *curvinervis* Zett., but this was considered by Villeneuve to be a synonym of *trepida*. Owing to the conditions of the specimens the determination cannot now be checked.

region, which is very short. The head bears a remarkable group of 6 large circular sensoria; the felt-chambers are stout with flattened spiracular areas and sometimes strongly pigmented. The species *sequax* Will. and *prunaria* are extremely similar but differ from *spathulata* in having larger sensorial organs (Figs. 17, 18). It may be noted that the larva of *Petina erinaceus* has a similar mouth-hook, though it has only two cephalic sensoria.

The primary larvae of *Wagneria succincta*, *Kirbya moerens* and *Phorichaeta atra* (cf. the Manual of Myiology) are altogether different and are all of the same type. The buccopharyngeal armature is of the characteristic voriine form and the peculiar cephalic sensoria are wanting. The larva of *Kirbya moerens* has on the anterior region of the buccopharyngeal armature, a remarkable pointed tooth, which seems to be set in a socket near the dorso-anterior border, not far from the apex. If the larva is roughly handled, this tooth becomes detached. A similar tooth, perhaps not quite as well differentiated, exists in *Wagneria succincta* and it is shown very distinctly in Townsend's figure of the mouth-hook of *Phorichaeta atra*. Finally—and what is most surprising—this tooth is very well developed in the larva of the voriine *Klugia marginata*. The figures (22, 25) show how similar the structures are. The peculiar tooth does not exist in the other voriines examined. It may be noted that Robineau-Desvoidy separated *Klugia* from them.

It appears to me that this extremely close resemblance in a characteristic larval morphology cannot be the result of random variation in individual characters but indicates a fundamental natural affinity. It seems justifiable to conclude that *Klugia marginata*, *Kirbya moerens*, *Wagneria succincta* and the species figured by Townsend as *Phorichaeta atra*, form a natural group, whose place is with the voriines.

B. Herting (1957), following his comprehensive study of the female terminalia of the tachinids, places with the voriines (s. lat.) a number of genera not mentioned above: *Eriothrix* Meig., *Phyllomyia* R.D., *Campylochaeta* Rond., *Blepharomyia* B.B., *Redtenbacheria* Schin., *Thelaira* R.D., *Phoenicella* R.D. Herting notes that while Verbeke places *Eriothrix* here—presumably because of the form of the male genitalia—he himself finds it difficult to classify, considering the form of the female genitalia.

I have examined the primary larvae of *Eriothrix*, *Phyllomyia*, *Campylochaeta* and *Thelaira*. The larval morphology of *Eriothrix* is quite distinctive and it cannot be classed with either the voriines or the wagneriines. *Phyllomyia* has a long curved mouth hook, very elongate and slender felt-chambers and 7 very heavy, short, ventral spine bands. It is certainly closer to *Wagneria* than to *Voria* but its affinities remain doubtful. *Campylochaeta* has mouth parts very much like those of *Wagneria* which it also resembles in the form and color of the posterior " felt-chambers " which are dark and notably flattened at the ends. *Thelaira*, on the contrary, has mouth parts much like *Klugia*, having the lateral plates fused dorsally within the roof of the mouth so as to form a kind of cap. The anterior region is quadrate, with the characteristic voriine striping. A peculiarity of this larva is a heavy triangular plate in the middle of the ventral side of segment I.

To what extent the affinities suggested above can be expressed in terms of adult characters, remains to be seen. Many of the forms mentioned above as showing primary larvae of the voriine type do not correspond to the definition given in this paper covering the three Trinidad voriines.

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I am very grateful to the Canadian National Research Council in Ottawa and to the Royal Society of London for the provision of funds permitting me to carry on work in Trinidad and to contribute to the cost of the publication of results. The authorities of the United States National Museum in Washington kindly allotted space and gave permission to use the Tachinid collection in the identification of material. Dr. C. W. Sabrosky gave most valuable help during the course of this work. In Trinidad, through the kind help of Professor J. H. Purseglove, Dean of the Faculty of Agriculture of the University College of the West Indies, space for work and living accommodation were secured in a location especially suitable for our studies. Mr. F. D. Bennett, of the Commonwealth Institute of Biological Control assisted in the collections on many occasions and provided much useful material. I must gratefully acknowledge also the all-important assistance of my wife who has prepared the majority of the drawings for this paper. Finally I wish to thank the American Entomological Society for permission to publish the studies on the Trinidad Tachinids in its Transactions, and the Editor, Mr. Harold J. Grant, Jr., for his helpful advice.

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Explanation of Figures

Plate I

Fig. 1.—*Voria ruralis* Fall. Buccopharyngeal armature, stage I. AR—anterior region, a median unpaired sclerite; IR—intermediate region; PR—posterior region with ventral and dorsal wings; LS—lateral sclerites, the homologues of the paired mandibles in stages II and III, when these are differentiated; SD—sclerite of the duct of the salivary gland.

Fig. 2.—*Voria ruralis* Fall. Head of adult, side view.

Fig. 3.—*Voria ruralis* Fall. "Felt-chambers" and posterior spiracles, stage I.

Fig. 4.—*Voria ruralis* Fall. Buccopharyngeal armature, stage II. The mandibles are fused dorsally and ventrally into a hollow cylinder.

Plate II

Fig. 5.—*Minthoplagia rafaeli* T.T. Buccopharyngeal armature, stage I.
Fig. 6.—*Eucyrtophloeba horrida* G.T. Head of adult, side view.
Fig. 7.—*Minthoplagia rafaeli* T.T. Spine group of one of the posterior segments, stage I.
Fig. 8.—*Athrycia trepida* Meig. Posterior spiracles and adjacent sensoria, stage III.
Fig. 9.—*Athrycia trepida* Meig. Larva, stage I *in situ* in muscle fibre of its lepidopterous host. L—larva.

Plate III

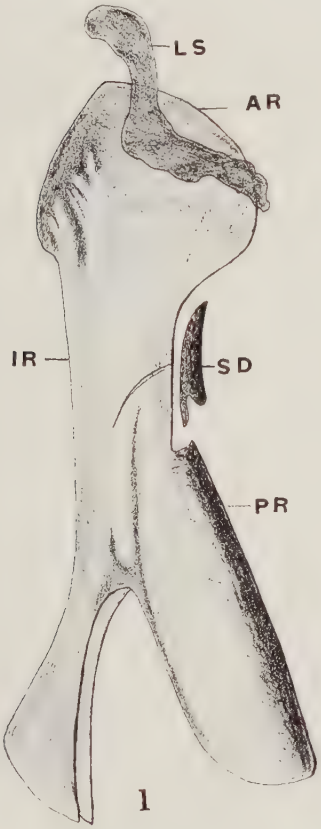
Fig. 10.—*Voria ruralis* Fall. Felt-chambers and posterior spiracles, stage II.
Fig. 11.—*Voria ruralis* Fall. Posterior spiracles, stage III, simplified from H. L. Parker.
Fig. 12.—*Voria ruralis* Fall. Buccopharyngeal armature, stage III.
Fig. 13.—*Minthoplagia rafaeli* T.T. Head of adult, side view.
Fig. 14.—*Voria ruralis* Fall. Puparium, showing anterior and posterior spiracles, after Greene.

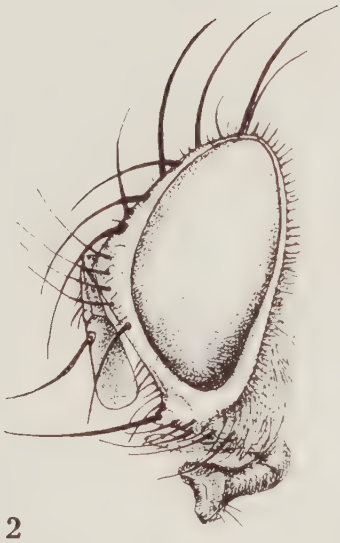
Plate IV

Fig. 15.—*Athrycia trepida* Meig. Buccopharyngeal armature, stage II.
Fig. 16.—*Athrycia trepida* Meig. Anterior spiracle, stage III.
Fig. 17.—*Wagneria sequax* Will. Pair of cephalic sensoria, stage I.
Fig. 18.—*Wagneria spathulata* Fall. Pair of cephalic sensoria, stage I, same magnification as 17.
Fig. 19.—*Athrycia trepida* Meig. Longitudinal section of last segment of stage I larva, in dorso-ventral plane. ID—imaginal disc; RV—rectal vesicle, showing interior part of intestine and muscle to invaginate vesicle; S—spiracle and felt-chamber.
Fig. 20.—*Athrycia trepida* Meig. Larva, stage II, showing arrangement of cuticular spines.

Plate V

Fig. 21.—*Athrycia trepida* Meig. Buccopharyngeal armature, stage III.
Fig. 22.—*Kirbya moerens* Meig. Buccopharyngeal armature, stage I.
Fig. 23.—*Wagneria prunaria* Meig. Buccopharyngeal armature, stage I.
Fig. 24.—*Eucyrtophloeba horrida* G.T. Buccopharyngeal armature, stage I.
Fig. 25.—*Klugia marginata* Meig. Buccopharyngeal armature, stage I.





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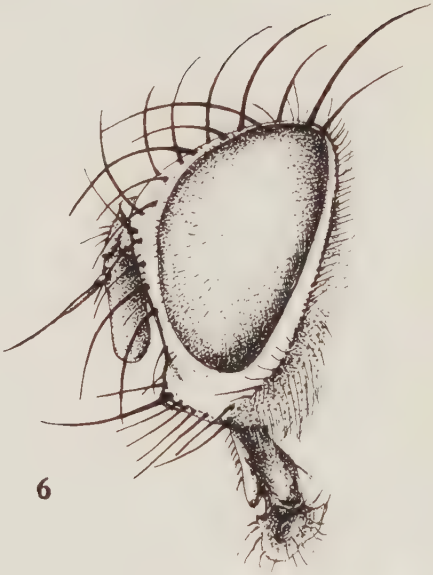

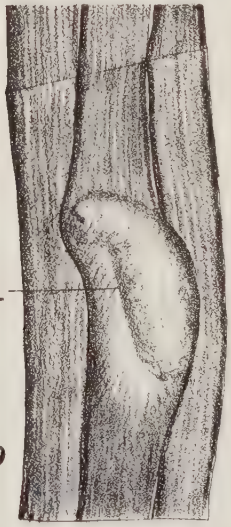

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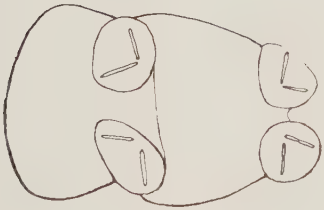

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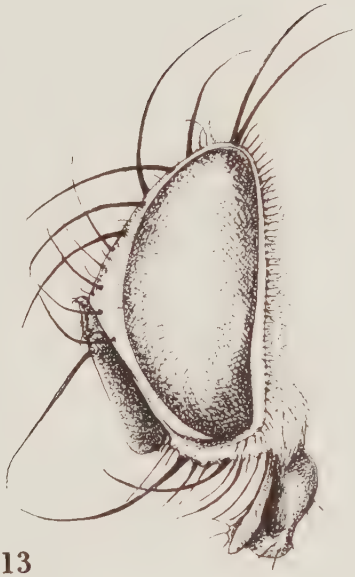

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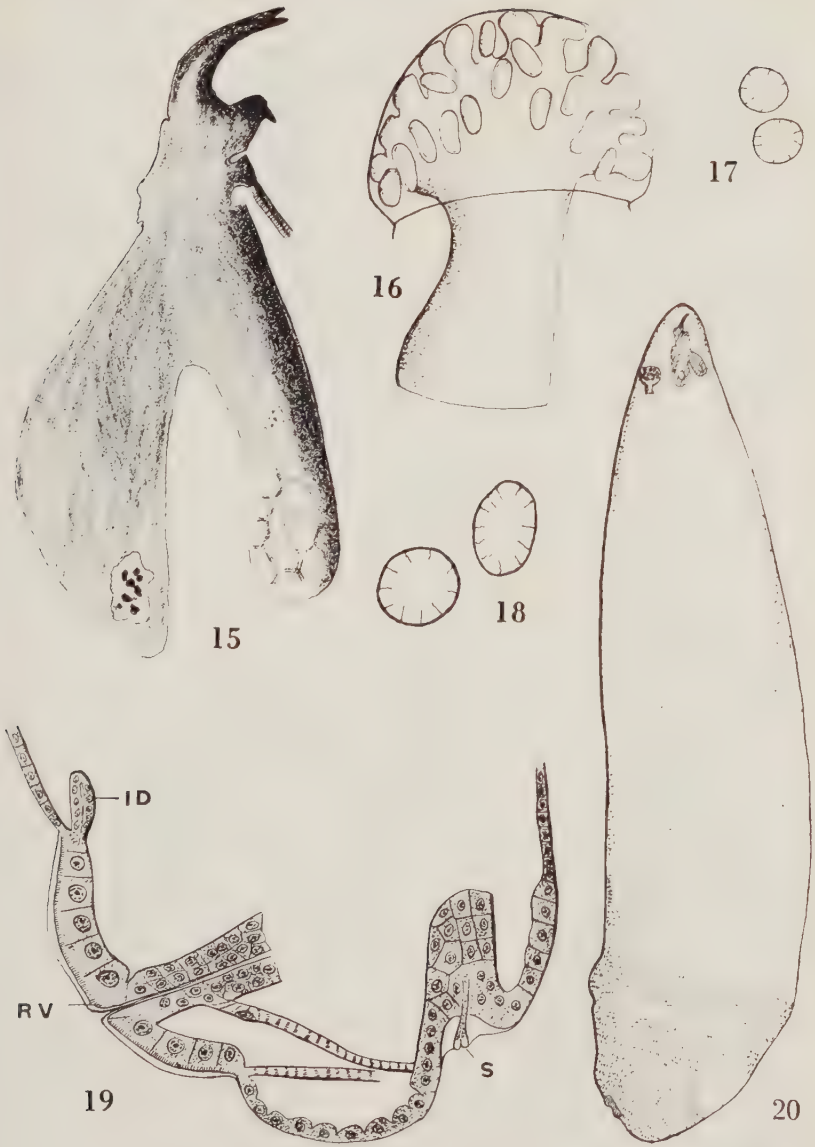

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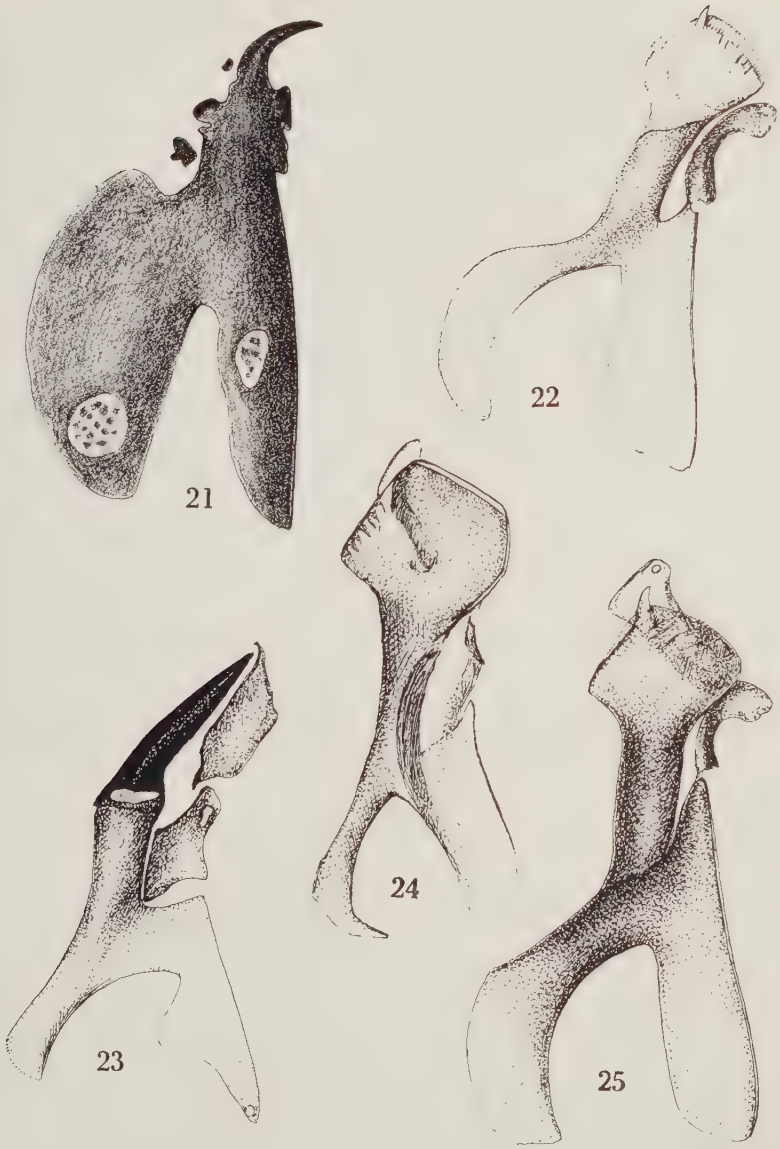

THOMPSON: TACHINIDS OF TRINIDAD

THE REPUGNATORIAL GLANDS OF THE TENEBRIONID BEETLE (COLEOPTERA) ELEODES OBSOLETA (SAY)

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Although odoriferous organs are distributed extensively throughout the animal kingdom they seem to be most common among arthropods, particularly in the terrestrial air-breathing forms such as the insects. In this group the glands frequently occur as simple hypodermal pouches which are capable of releasing variable quantities of highly volatile and noxious fluids.

An early classification of odoriferous glands in insects was made by Packard (1895), when he divided all scent-producing organs into repugnatorial and alluring. A third class including those for recognition only was suggested by McIndoo (1917). Among these three classifications it is the author's belief that the term repugnatorial would best apply to the odoriferous glands of *Eleodes obsoleta* (Say).

Wade (1921) listed all known families of Coleoptera that possess odoriferous glands. His summary includes such families as Cicindelidae, Carabidae, Staphylinidae, Meloidae, and Tenebrionidae. The catharidine in some species of Meloidae has been demonstrated to be a particularly caustic agent capable of repelling insects, birds, and some small reptiles (Melander and Brues 1907). The body fluid itself (produced by "reflex bleeding" in the Coccinellidae) has been reported to serve as an effective repellent against predaceous insects (McIndoo 1916). In the family Carabidae the "Bombardier Beetle" (*Brachinus*), which releases a secretion from the end of its abdomen with controlled accuracy, has been shown to be capable of repelling ants, carabids, mantids, and spiders (Eisner 1958). It was reported earlier that the discharge was accompanied by a puff of vapor and an audible report (Packard 1895).

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The presence of odoriferous glands has been demonstrated in several species within the genus *Eleodes*, including *E. extrica*, *E. vandykei*, *E. dentipes*, *E. acuta*, *E. longicollis*, *E. suturalis*, *E. hispilabris*, *E. tricostata*, *E. giganti* and *E. obsoleta* (Summary publication, McIndoo 1917, and personal observations 1959 and 1960). Most of the work pertaining to the above listed species was performed between 1823 and 1922. The recognition of these glands was for the most part subjective, based on expelled odors, and fluids on various types of substrates.

More recently Eisner (1958), Eisner and Blumberg (1959), Roth (1943, 1945), Roth and Howland (1941), Roth and Loconti (1953), Roth, Niegisch and Stahl (1956), Roth and Stay (1958), Stay (1957) have made morphological studies of odoriferous glands and the chemical nature of the glandular secretion in several families of Coleoptera and Orthoptera. Eisner (unpublished 1959), expanded his work into the field of comparative behavior in his experiments pertaining to the relation between invertebrate and vertebrate predators and the defensive secretion of arthropods. His work was performed to determine the survival value gained by organisms possessing these glands. There are, however, few cases in which a comprehensive study of one species has been made. This study is an investigation of the repugnatorial glands of the tenebrionid beetle *Eleodes obsoleta* (Say), dealing with those factors that play a role in the functional operation of the glands.

Methods.—All beetles used in this study were collected two miles south of the United States Bureau of Standards, Route 93, Boulder, Colorado. Collections were made between September 23 and October 30, 1959, and between August 6 and October 24, 1960. Representative individuals of *E. obsoleta* were identified by T. J. Spilman, National Museum, Washington, D. C. Specimens have been deposited under the author's label at the Henderson Museum, University of Colorado.

The collection site was delimited to an area of 350 square yards (70 yds. by 5 yds), and is located within a typical Colorado plains region. The plains extend approximately one mile westward to the foothills of the Rocky Mountains.

Beetles were confined in the laboratory to a wooden cage (27″ × 27″ × 5″) covered by wire screening. A habitat similar to that of the collection area was restored by covering the floor of the cage with a substrate of material found in the field. A supply of water, lettuce, dog chow, and oat meal was present at all times.

The repugnatorial glands were dissected from beetles killed in ether. The last abdominal sternite was gently pulled with a pair of watch-maker's forceps and was torn from the body. The glands, swollen with secretion, were cut off and the glandular tissue was fixed in Bouin's solution, followed by dehydration and embedding by the Tertiary Butyl Alcohol method. The tissue was then cut at ten micra and stained in Foley's Variation of Heidenhain's Modification of Mallory's Triple Stain.

The secretory discharge was recorded on cobalt chloride indicator paper. Standard filter paper was saturated with 50 percent cobalt chloride solution and dried. The paper in this condition is light blue; however, when exposed to a solution containing water, the paper turns pink in the contact area. The secretion of *E. obsoleta* contains a small amount of water and gives a positive reaction to this test.

A beetle was fitted with a small hook fastened to the pronotum with ferrule cement, and attached to a wooden rod, using small couplings of polyethylene tubing; the free end was held in a universal clamp to allow the beetle to assume a normal stance on the indicator paper. The beetle was then mechanically disturbed by pulling one of its hind tarsi with a pair of watch-maker's forceps. This action would usually cause two droplets of secretion to appear on the tip of the beetle's abdomen, permitting contact between the indicator paper and the fluid.

The repugnatorial secretion was collected from 342 beetles. An aspirator attached to a laboratory water tap swept air through a collecting system. The air, dehydrated in a Drierite unit, entered a one liter Erlenmeyer flask which contained the beetles. The volatilized beetle secretion was picked up in this chamber and was carried into a spiral collection trap immersed in a Dewar flask containing dry ice dissolved in "Cellosolve" (ethyl glycol monobutyl ether). The dry ice mixture maintained the trap at

a constant – 79° C. The temperature depression was sufficiently low, causing the secretion to crystallize out onto the walls of the spiral glass tubing. The flow of air then passed into a second Drierite unit, a second Erlenmeyer flask and out of the system through the aspirator. The second Drierite unit prevented moisture from re-entering the system, while the second flask served to catch the overflow water from the aspirator.

The system ran for a period of four hours. During this time the flask containing the beetles was shaken for a period of one minute, 15 times. The flask was immersed alternately in hot (80° C.) and cold (10° C.) water with the same frequency and time duration. When the collection period was terminated the trap was sealed and warmed to room temperature. The secretion was then dissolved in carbon tetra-chloride, filtered, and pumped by means of a hypodermic needle into a 1 millimeter liquid phase Beckman Infra-red Photospectrometer cell. A second cell containing only the solvent was prepared as a blank, and an analysis of the secretion was made.

Adult life cycle.—The author has not encountered any discussion of the life cycle of *E. obsoleta* in Colorado. It would seem most probable that the adult life cycle is relatively short, beginning in the early part of August, declining rapidly in September, and ending in late October. This statement is based on the author's inability to collect any large number of beetles before August and the fact that in the laboratory, larval forms appeared at the end of May 1960. Unfortunately the larvae failed to pupate so that complete laboratory substantiation of the life cycle cannot be established. (Larval forms were not looked for or found by accident in the field.)

The majority of the population is killed off in October with a few adults overwintering underground. Substantiating this, a greatly increased number of dead beetles was found at the time of population decline. That a certain number overwinter is suggested by the limited amount of beetles collected before the August population increase. It is therefore hypothesized that, (1) eggs are layed during the months of August, September and October, (2) the eggs overwinter and undergo development to the larval stage during the month of May, (3) pupation occurs sometime in early June, and (4) the adults first appear in August and breed through August, September and early October.

Gross morphology of the repugnatorial glands.—The position of the repugnatorial glands of *E. obsoleta* was first indicated in the field. When picked up, the beetle released two droplets of secretion which appeared on the lower surface of the last abdominal sternite. Dissections were performed on 40 specimens to determine the location, morphology, and structures associated with the glands.

Initial dissections in the abdominal region revealed secretory glands which ranged in size from 1.2 mm. to 2.5 mm., the larger structures being found in the females. The distal ends of the paired organs are attached to a thin strip of cuticle which is continuous with that of the last abdominal segment. The proximal extremity extends to the sutural connection between the third and fourth abdominal sternite. In this region the glands lie on either side of the intestine, while more posteriorly they are situated beneath the genital organs. The glands are separated from these organs by a sheet of tissue which is attached to the border of the last abdominal segment.

The portion of the glands that extends into the intestinal region is surrounded by a dense accumulation of fat bodies. The tracheal anastomosis near the anterior region of the last abdominal segment sends out branches which course beneath the fat bodies, ramifying extensively over the surface of the glands.

A series of transverse striations occur on the surface of the glands. However, when they are distended with fluid these markings are barely visible. The oily fluid within the cuticular sac is brown in color. It extends throughout the sac to a narrow duct leading to the border of the last abdominal segment. The fluid is restricted at this point by a mechanism that shall be discussed in the following section on histology. The ducts continue for a short distance, eventually opening into small pores which make contact with the outside (Fig. 1).

Histological morphology of the glands.—The histological nature of the tissues that compose the repugnatorial glands of *E. obsoleta* are demonstrated in a schematic diagram (Fig. 2) which is supplemented by photomicrographs of specific tissues (Figs. 3 and 4).

The glands are cup-shaped invaginations that remain in direct contact with the epidermis of the body wall. The epidermis (hypodermis) is continuous externally with the three layered cuticula (epicuticula, exocuticula and endocuticula) which it secretes (Snodgrass 1935). Internally the epidermis rests on a thin non-cellular basement membrane.

The cuticular layers are modified medially, curving inward to form the duct of the gland. The duct extends anteriorly into the body of the gland itself forming an extremely thin cuticular intima, which is continuous with the secretory cells. This lining is interrupted periodically and sends out variable numbers of minute capillary ductules to the secretory cells.

The secretory cells are highly lobate. They possess a granular nucleus of circular shape, which is variable in position. Snodgrass (1935) states that the nucleus of this type of structure is, "probably the source of the substance that activates the secretory properties of the cytoplasm." There are usually within the cytoplasm two thick-walled vacuoles of variable size and shape. Richards 1951, in his discussion on specialized glands associated with the development of the cuticle, states that epidermal glands are capable of "accumulating a secretion in a vacuole which grows and coalesces, and having secretion poured out an intracellular duct extending through the cuticle." This type of situation undoubtedly occurs in the glands presently under discussion, for within the cytoplasm arise non-cellular capillary ductules which extend medially and join the cuticular intima lining the cavity of the gland. This lumen in an undisturbed insect serves as the major storage area for the product of the secretory cells.

Minute tracheal respiratory branches which serve the metabolically active cells are found in the intercellular spaces.

Located just anterior to the cuticular layer and surrounding the duct of the gland is a series of striated muscles. These muscles, which run parallel to the long axis of the gland, send out fine connective fibrils, tonofibrillae, which traverse the epidermis and attach to the cuticula. The probable function of these muscles will be discussed later. Finally, the whole gland is encased in a cuticular sac that possesses numerous ridges. The presence of these ridges gives a striated appearance to the surface of the glands as described in the previous section.

Mechanism for discharging the secretion.—The secretion of *E. obsoleta* was recorded on cobalt chloride indicator paper. When the beetle is mechanically stimulated, two droplets of secretion appear on the tip of the last abdominal sternite. The fluid remains on the abdomen for approximately 15 to 25 seconds and then volatilizes. The secretion is capable of turning the blue indicator paper pink in the contact area (any solution containing water will do this) thereby demonstrating the exact position of the secretory release. During fifteen tests there was no indication of any directional control of the repugnatorial secretion.

Investigations relative to the gross and histological nature of the glandular tissue present one possible morphological control over the secretory discharge. The striated muscles located in the duct region of the gland are probably functional in releasing the secretion from the cavity of the glandular sac. Since the fibrils run parallel to the long axis of the gland, as do the muscles themselves, contraction of the fibrils would draw the gland posteriorly, thereby compressing the fluid within the glandular sac. At this point a droplet of secretion would pass down the duct and eventually appear on the tip of the last abdominal sternite. This is substantiated in that the amount of fluid that appears externally is small compared to that present within the sac itself.

In conjunction with the controlling effect of the striated muscles, it would seem probable that the general contraction of the organs in the abdominal region, as would occur when the insect was placed under stress, would help force the fluid out by compressing the sac within which it is contained.

It should be noted that sphincter muscles were not found. The exact mechanism for containing the fluid within the sac while a beetle is at rest was not determined. However, the normal tissue pressure in the duct region may be sufficient to block the flow of fluid to the outside.

Chemical composition of the secretion.—The secretion of *E. obsoleta* resembles in color and odor the para-quinone secretion of the cockroach *Diploptera punctata* (personal observations, 1959).

When the secretion is placed in concentrated sulfuric acid it becomes dark red. When added to 10 percent potassium hydroxide, the fluid becomes green. In a final test the yellow secretion

gave a blue-black color when placed in contact with potassium iodide starch paper. In each case the reaction was identical to those reported by Roth and Stay (1958), in their preliminary experiments which eventually led to their successful identification of the para-quinone secretion of *D. punctata.*

Further qualitative tests were made with the aid of infra-red photospectrometer analysis. The secretion demonstrated peaks at 3.40, 3.48, 5.76, 6.00, 8.89 and 9.31 micra. The strongest and most significant of these peaks were located at 5.76 and 6.00 micra. This is the position of the quinone carbonyl absorption characteristic of the α-B, α'-B′ diaryl ketone (Bellamy 1958).

The peaks at 3.40 and 3.48 micra are indicative of the carbon-hydrogen bond, thereby showing the presence of alkl suybstituted quinone. However, the specific alkyl group was not determined.

The final areas of absorption at 8.89 and 9.31 micra are also present in the spectra in alkyl substituted benzoquinone. Roth and Stay (1958), found in their analysis of the secretion of *D. punctata* that a mixture of 2-methyl-1,4-benzoquinone; 2-ethyl-1,4-benzoquinone, was located in these areas.

The repugnatorial secretion of *E. obsoleta* is therefore a quinone compound possessing alkyl groups. This, however, is not a complete analysis of the secretion.

Discussion.—This study was performed to investigate the repugnatorial glands of the tenebrionid beetle *E. obsoleta,* incorporating those factors that play a role in the functional operation of the glands.

Repugnatorial glands represent a major defensive mechanism within the genus *Eleodes* as demonstrated by the large number of species that possess such organs, and associated behavioral patterns that permit them to function efficiently. The defensive stance so typical of the genus (a beetle will stand with its head pointed downward at approximately a forty-five degree angle while releasing two droplets of secretion from the tip of its abdomen) is a direct adaptation to a ground dwelling habitat and slow movements. Once a beetle is exposed from a sheltering rock the stance grants maximum protection, since the glands themselves are located on the last abdominal sternite.

The secretion of *E. obsoleta* was shown to be a quinone compound possessing alkyl groups. Similar compounds have been demonstrated to be defensive devices in several genera of Tenebrionidae, and in a variety of millipeds, phalangids, cockroaches, earwigs and carabids (Eisner and Blumberg 1958). Quinones are caustic tanning agents capable of causing lachrymation in humans, either by direct contact or by exposure to the vapors. When placed on the tongue one experiences a strong burning sensation. It is imagined that a predator would undergo the same "unpleasant" sensation when coming in contact with the secretion and eventually learn to avoid an organism possessing this type of defense.

This was shown to be the case in the laboratory when the frog *Rana pipiens* learned to reject a normally colored intact *E. obsoleta*. When introduced to a situation involving choice between this normal beetle and a glandless one with its elytra painted white, the predator did not attack either of the prey. At this point *Tenebrio molitor* larvae were used to test whether the frog had attained a sufficient hunger level to feed. Since a larva was eaten in each trial there can be no doubt that the lack of predation in the previous set of experiments was due to a factor other than hunger.

In two other sets of experiments, the intact beetle was rejected for 10 trials, followed by successful predation upon glandless beetles for 10 trials. This gives strong evidence that not only will *R. pipiens* reject an intact normally colored beetle, but that the presence of this insect will inhibit the frog's ingestive behavior upon a glandless beetle with elytra painted white, which it will accept as a source of food when it is introduced alone.

The experimental situation was improved in behavior studies involving the lizard *Crotaphytus collaris* and the mouse *Peromyscus maniculatus,* by establishing a true situation involving choice. The results show that both of these predators are capable of discriminating against a normally colored beetle with glands intact, and that in a situation involving a choice, a glandless beetle with elytra painted white will be selected. When manipulating the colors so that the glandless beetle is normally colored and the intact beetle has its elytra painted white, the predators after several trials will select the glandless beetle.

It is the author's opinion that these experiments demonstrate that the repugnatorial secretion of *E. obsoleta* has a high degree of survival value. Furthermore, it is speculated that in a natural situation where a large choice of insect food is available, a vertebrate predator such as those used in this study would, after contact with the secretion, select another organism as a source of food, thereby contributing to an individual's survival, and to the species as a whole.

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EXPLANATION OF FIGURES

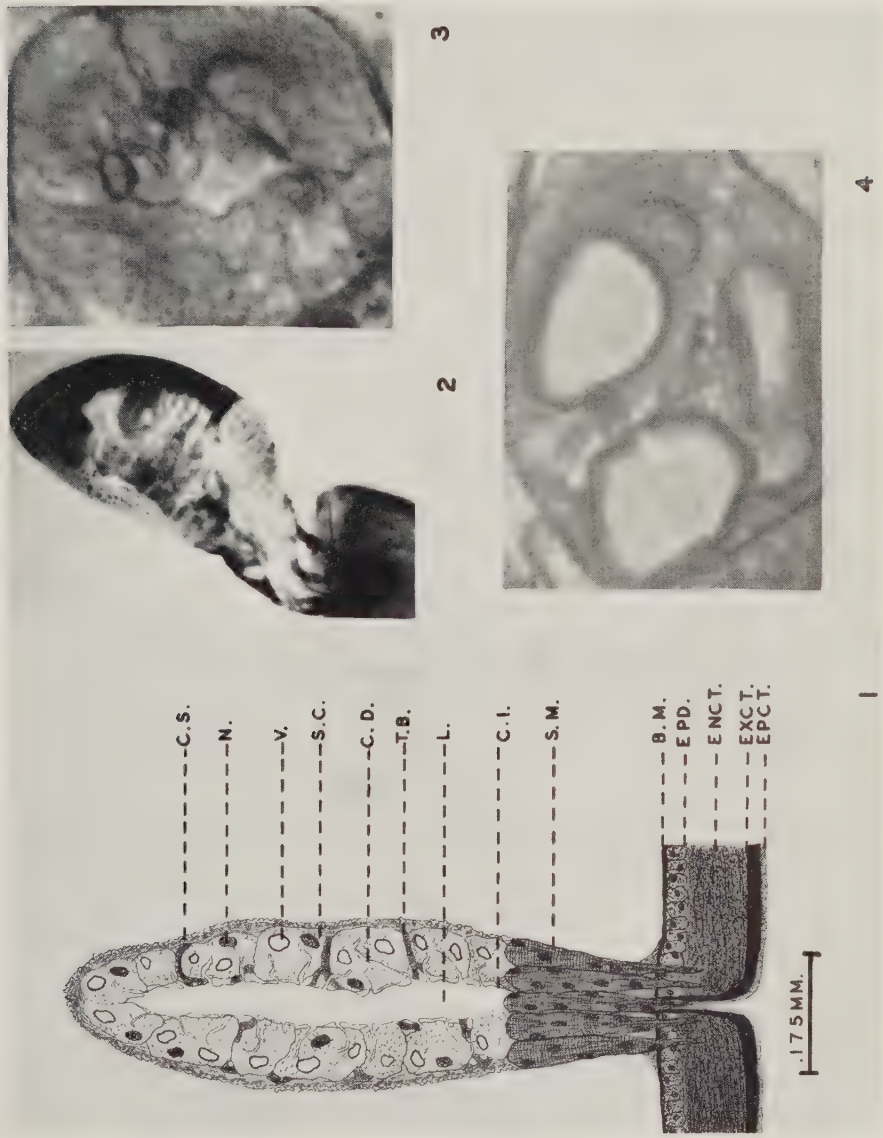
PLATE VI

Fig. 1.—Photomicrograph of a repugnatorial gland attached to a strip of cuticle which is continuous with that of the last abdominal sternite. ×50.

Fig. 2.—Schematic diagram of the histological morphology of a repugnatorial gland: B.M., basement membrane; C.D., capillary ductule; C.I., cuticular intima; C.S., cuticular sac; ENCT., endocuticula; EPCT., epicuticula; EPD., epidermis; ENCT., exocuticula; L., lumen; N., nucleus; S.C., secretory cell; S.M., striated muscle; T.B., tracheal branch; V., vacuole.

Fig. 3.—Photomicrograph of a secretory cell showing three capillary ductules arising from the cytoplasm surrounding a vacuole (clear center). Cross section ×1320.

Fig. 4.—Photomicrograph of a secretory cell showing two clear oval, thick-walled vacuoles, and a single circular, granular nucleus. Longitudinal section ×1333.



BLUMBERG: TENEBRIONID REPUGNATORIAL GLANDS

TIPHIA OF CUBA AND HISPANIOLA (HYMENOPTERA, TIPHIIDAE)

BY H. W. ALLEN [1] AND KARL V. KROMBEIN [2]

The present study was undertaken to clarify the taxonomy of the species of *Tiphia* occurring in Cuba and Hispaniola by redescription of the two previously known species and description of six additional new species. No other genera of Tiphiidae are known to occur in this area except for *Myzinum* whose species were revised by the second author in two earlier contributions.[3]

Association of sexes in Tiphiidae is always a difficult problem because of the high degree of sexual dimorphism. The males of many species of *Tiphia*, occurring in such widely separated areas as Argentina, the Antilles, and North America, have a prominent transverse carina anteriorly on the dorsum of the first abdominal tergum. Frequently this character is associated with an elongated radial cell in the forewing. In Cuba and Hispaniola males having these characters appear most probably to be associated with females in which the hind basitarsus is *not* grooved. In North America males with these two characters have been associated only with females in which the hind basitarsus is grooved. The problem of association of sexes in the Cuban and Hispaniolan species is additionally complicated by the fact that females of *wolcotti* and *haiti*, which do possess the basitarsal groove, have been taken at the same locality and on the same date as males of *hispaniolae*, which have the elongate radial cell, and a transverse carina on the first tergum. However, there is little doubt as to the association of sexes in the Cuban *argentipes*, in which the female lacks the basitarsal groove and the male has

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the tergal carina and elongate radial cell. Therefore, we have felt that the association of sexes in *hispaniolae,* proposed by Wolcott and based on similar characters in the two sexes, should be maintained unless and until additional evidence proves this association to be erroneous.

The following abbreviations have been used: United States National Museum (U.S.N.M.); Academy of Natural Sciences of Philadelphia (A.N.S.P.); Harvard College Museum of Comparative Zoology (M.C.Z.); Research Laboratory of the U. S. Department of Agriculture at Moorestown, N. J. (M.).

Tiphia hispaniolae Wolcott

Tiphia hispaniolae Wolcott, Univ. of Puerto Rico Jour. Agric. 22: 189–192. 1938.

Male.—Front with punctures coarse, deep, contiguous laterally to upper corner of eye, and medially except for a narrow strip the width of an ocellus below anterior ocellus; dense secondary punctures laterally extend upward into lower part of upper half. Cheeks in unrubbed specimens with appressed white hairs; distinctly narrower than diameter of an antennal fossa. Clypeus with its median extension about one and one-fourth times as long as wide, usually with apex more emarginate than bidentate, and margin polished and impunctate one-fifth the distance to base; lateral carina rolled, and at one point only barely overhanging the moderate lateral pit. Mandible with a small, inconspicuous cusp on upper margin near the apex.

Dorsum of pronotum with a high, transverse carina; punctate portion with round, deep punctures of first- and second-degree density, secondaries lacking; impunctate apex medially scarcely half as long as punctate portion. Mesepisternum having almost no secondary punctures on its outer disc. Legs predominantly black. Hind tibia on inner face with a bare polished rib extending over nearly its full length; major calcarium prominent and distinctly widest near middle. Tegula black, polished, without a marginal groove along outer margin. Wing with lateral extension of radial cell greatly exceeding that of the second cubital; radial cell strongly infumated.

First abdominal tergum with a strong transverse carina anteriorly, the preapical band of rather large, nearly contiguous punctures, somewhat impressed, and generally as wide as the diameter of a puncture except for scattered ones medially out of line. First sternum with coarse, shallow sculpturing bordering the lateral carina. Other intermediate terga with rather fine, uniformly distributed punctures, without well-defined discal impunctate areas on third tergum and those following. Second sternum with an anteromedial impunctate callosity, best seen in profile. Fifth

sternum without lateral denticle or ridge. Pygidium with an impunctate median vitta. Sixth sternum with the terminal crotch having the prongs of bifurcation sharp and more or less rounded in cross section.

Length, 7 to 10 mm.

Female.—Front on upper half coarsely punctate, punctures largely second-degree, secondaries almost lacking. Clypeus with median extension subtruncate, as long as diameter of antennal fossa, polished impunctate on an even apical band two-thirds distance to base of antennae; lateral carina not sharply folded, and only slightly overhanging the lateral pit, which is subobsolete since it lacks a lower margin except in the side of the median extension. Mandible with a well-developed medial groove.

Dorsum of pronotum with anterior portion sparsely beset with coarse primary punctures of third-degree density on lateral discs, but conspicuously concentrated in an irregular row at margin of the impunctate apex; large secondaries about as numerous as the primaries. Mesepisternum conspicuously shagreened; primary punctures on disc widely scattered, separated by distances several times their average diameter; secondaries large and about as numerous as primaries. Legs black. Hind tibia with lower half of inner face at most with a few sparse hairs, its upper margin not elevated at line of contact with the densely setulose area. Hind basitarsus on inner face, evenly convex, nearly bare on basal half, apex with a conspicuous patch of dense short white hairs and a comb of six equal dark-brown bristles set between larger bristles; without trace of longitudinal groove. Tegula black, without a marginal groove, very faintly shagreened. Wings strongly infumated.

Areola subrectangular, about two times its greatest width. Posterior aspect of propodeum coarsely granular reticulate over the whole surface. First tergum with preapical band of very fine punctures, not impressed, and medially about one row wide. First sternum flat and microscopically setulose, with lateral groove continuous to escutcheon, and without other coarse sculpturing. Terga 2, 3, and 4 with wide impunctate areas laterally, and with polished impunctate apices medially several times the diameter of nearest adjacent primaries. Pygidium punctate on basal half; impunctate portion conspicuously shagreened to near apex.

Length, 12 to 16 mm.

The type, a male, is deposited in the U. S. National Museum. The species has been redescribed from the type, several paratypes, and other specimens identified by Wolcott (U.S.N.M. and M.). Since Wolcott included at least three species in this material we have listed below the specimens we consider to be *hispaniolae*. All were collected by G. N. Wolcott in Haiti. Kenscoff, 1 ♂, April 26, 1927; 3 ♂♂, paratypes, and 3 other males, Haiti no. 59-27, November 23, 1927; 2 ♀♀, paratypes, and 2 other

females, acc. no. 133-37; 2 ♂♂, type and paratype, December 13; 3 ♂♂, January 21–31, 1948. Port Chaubert, Le Trou, 1 ♂, November 10, 1927.

There are also four somewhat smaller males (M.) with browner legs and finer punctation which probably belong here. They were collected with other males of *hispaniolae*. One is from Mt. Puilsboreau, No. 11, lot 59-27; 2 from Kenscoff, November 23, 1927, lot 59-27; and 1 from Kenscoff, January 21–31, 1948.

Tiphia kenscoffi new species

This species is similar to *hispaniolae* in the characters used in the redescription, except as follows. The first tergum has no anterior transverse carina, although in some specimens there is an obscure, irregular transverse break in the contour in that area. The preapical band of punctures is more dispersed, not impressed, and consists of moderately large discrete punctures, medially not narrowly aligned. The wing is hyaline, or nearly so; radial cell greatly exceeding second cubital.

Length, 6.0 to 8.5 mm.

Type.— ♂, Kenscoff, Haiti, Haiti no. 59-27, April 26, 1927 (G. N. Wolcott) (U.S.N.M. Type No. 65698).

Paratypes.—6 ♂♂, same information as the type, (M.) and (U.S.N.M.).

Female.—Not known.

Tiphia sandae new species

Male.—This species differs from our redescription of *hispaniolae* as follows. The disc of the mesepisternum is densely beset with minute punctures which are much more numerous than the primaries. The posterior and anterior abscissae of the second cubital cell are about equal, whereas in *hispaniolae* the anterior abscissa is usually slightly longer; radial cell slightly exceeding the second cubital. The posterior aspect of the propodeum has a thin high carina on the lower half or more, which is absent in *hispaniolae*. The first tergum has a strong transverse carina anteriorly and a conspicuous polished impunctate transverse area anterior to the preapical band of punctures, which is more abruptly convex than in *hispaniolae*. The tegula and terminal abdominal terga are highly polished without perceptible shagreening.

Length, 8.5 mm.

Type.—♂ labeled "San Domingo" (A.N.S.P.).

Paratypes.—2 ♂♂ with the same data as type (A.N.S.P.).

Female.—Unknown.

Tiphia wolcotti new species

Female.—Front with coarse, deep punctures, on upper half mainly of second-degree density with almost no minute punctures. Clypeus with its medial extension subtruncate, shorter than diameter of an antennal fossa, apical half a polished impunctate band; lateral carina well-developed, and overhanging the lateral pit at a point below the cheek. Mandible with a prominent medial groove. Palpi, and antennae beneath, fulvous.

Dorsum of pronotum usually with a weak carina interrupted medially; punctures coarse and usually sparse but not in the terminal transverse row where they are present as a narrow contiguous band. Mesepisternum on disc with moderate-sized punctures of third-degree density, the interspersed secondaries about as numerous as the primaries. Legs black. Hind tibia on inner face with lower portion sharply separated from the upper densely hairy patch by a slightly elevated margin; around the end of the sensorium the bare area is larger, more angular, and less clearly separated from the hairy area than in *haiti*. Hind basitarsus with a very shallow groove which is often less than half the length of the joint. Stout spines on edge of outer surface of hind tibia are usually reddish and partly translucent; the three stout spines on hind basitarsus are translucent yellow or reddish. Tegula black, sometimes faintly depressed on outside margin, never even faintly shagreened. Wing strongly infumated; stigma and nervures black, usually without a stump at apex of second cubital cell.

Areola subrectangular, or with sides straight and slightly convergent toward apex, usually about 2½ times as long as greatest width. Posterior aspect of propodeum unsculptured except for fine setulose punctures and very shallow primaries. First tergum with preapical band medially a single row of small primary punctures. First sternum without coarse sculpturing except the lateral groove which is usually continuous to the escutcheon. Terga 2 to 5 with rather fine, sparse punctures and broad impunctate spots on the discs; medially the nonmembranous apices are impunctate for a distance equal to several times the diameter of the larger adjacent primaries. Pygidium punctate on upper half, with a barely perceptible impunctate emargination; impunctate apex shading from orange to yellow, strongly shagreened to near apex.

Length, 10 to 13.5 mm.

Male.—Unknown.

Type.—♀, Kenscoff, Haiti, January 21–31, 1948, collector G. N. Wolcott, on *Daucus carota* (U.S.N.M. Type No. 65699).

Paratypes.—66 ♀♀, collected at the same time and place as the type. Several of these are deposited in the U. S. National Museum, and the Academy of Natural Sciences of Philadelphia.

We have also examined (U.S.N.M. and M.) the following female specimens collected by Wolcott at Kenscoff, Haiti. Acc. no. 133-27, 2 labeled as paratypes of *hispaniolae* U.S.N.M. type no. 52887, December 6 and December 13, 2 others on December 6, and 4 on December 13, 1937; acc. no. 58-27, 2 on November 23, 1927; P.R. acc. no. 5-46, 6 on December 1, 1946.

Tiphia haiti new species

Female.—Resembles *wolcotti* except as follows: Pronotum with punctures a little larger and usually of first-degree density over most of the punctate area. Tegula broadly shagreened. Hind leg with the stout spines on the outer edge of the tibia usually black and largely opaque, and the three stout spines of the basitarsus usually dark; hind basitarsal groove well-developed; area around sensorium of tibia a little smaller and more sharply separated from the setulose area.

Length, 10 to 13.5 mm.

Male.—Unknown.

Type.—Female, Kenscoff, Haiti, January 21–31, 1948, collector G. N. Wolcott, on *Daucus carota* (U.S.N.M. Type No. 65700).

Paratypes.—23 ♀♀, collected at the same time and place as the type. Several of these are deposited in the U. S. National Museum, and the Academy of Natural Sciences of Philadelphia.

Although collected at the same time and place as *wolcotti* this species differs sharply in the shagreening of the tegula. We have also seen two females collected by G. N. Wolcott; one, acc. no. 58-27, Mt. Puilsboreau, Haiti, November 11, 1927, and one acc. no. 58-27, Kenscoff, Haiti, November 23, 1927.

Tiphia paupi new species

Male.—Front, except for a narrow, impunctate vitta, with coarse, contiguous primary punctures to near level of lowest ocellus; upper half without many secondaries. Cheek scarcely masked with its vestiture of short white hairs; slightly wider than an antennal fossa. Clypeus with its median extension bidentate, with a very narrow, inconspicuous, impunctate apex; lateral carina thinly folded, but short and overhanging a short, moderately deep lateral pit. Mandibles without a cusp.

Dorsum of pronotum with its transverse carina complete and moderately high; punctate portion with its primaries rather uniformly distributed at distances slightly greater than their diameters; secondaries sparse. Side of pronotum when viewed from in front with a poorly defined groove across its disc. Mesepisternum on its disc, polished, with primary punctures of third-degree density, and secondaries slightly more numerous than the primaries. Legs black. Hind tibia with a prominent, narrow, naked rib extending the entire length of the inner face; apical calcaria yellowish. Hind basitarsus with a microscopic longitudinal ridge on basal half of inner face. Tegula piceous, without shagreening, or a groove on outer margin. Wing with radial cell in lateral extension much exceeded by the cubital cell, its apex directed strongly inward toward costal margin.

First tergum without a transverse carina or sulcate break on anterodorsal aspect; preapical band a single row of fine punctures in a straight and narrow line, moderately impressed. Second tergum with the usual short, parallel rugae of the anterior groove lacking on a wide median gap. Second sternum without a well-defined anteromedial polished callosity. Terga 3, 4, and 5 with the medial discal primary punctures moderately enlarged and dimpled, without impunctate areas; nonmembranous impunctate apices scarcely wider than diameter of largest adjacent primaries. Pygidium with a narrow, well-defined impunctate vitta extending to base of the segment.

Length, 7 mm.

Female.—Unknown.

Type.—♂, Port-au-Prince, Haiti, November 21, 1927, Haiti no. 59-27 (U.S.N.M. Type No. 65701).

The lack of a carina on the first tergite and the inwardly directed apex of the radial cell distinguish *paupi* at once from the males of *hispaniolae.*

Tiphia argentipes Cresson

Tiphia argentipes Cresson, Proc. Ent. Soc. Philadelphia 4: 117. 1865.

Female.—Front with moderate punctures of first-degree density upward to width of an ocellus from ocellar triangle, and with an impunctate median vitta. Clypeus with median extension subtruncate, about as long as diameter of an antennal fossa, with an apical polished impunctate band two-fifths distance to base of antennae.

Dorsum of pronotum shagreened, with scarcely a trace of a transverse carina; in restricted discal areas, punctures almost of third-degree density, but in a line bordering the impunctate apex they are contiguous. Mesepisternum with moderate punctures of third-degree density on a small area of outer portion. Legs piceous to black. Hind tibia on inner face with a longitudinal rib slightly raised at point of contact with the upper hairy section; sensorium concolorous with surrounding area, inconspicuous. Hind basitarsus without a longitudinal groove, nearly uniformly hirsute; apical

comb of bristles on inner apical margin not conspicuously differentiated from the dense white hairs. Tegula piceous, polished, without outer marginal groove, or shagreening. Forewing slightly infumated; second cubital cell without a well-defined apical stump.

Posterior aspect of propodeum shallowly, and irregularly sculptured at the sides, smooth in center except for the usual minute hairs. First tergum with rather weak setigerous punctures on outer anterior face; preapical band not impressed, consisting of one slightly irregular row of moderate, well-separated punctures. Other terga with punctures of medium size; terga 2 to 4 with wide impunctate areas; apices also medially impunctate for distances equal to 2 to 4 times width of largest adjacent punctures. Pygidium punctate on apical half; impunctate apex wrinkled, and only very faintly shagreened.

Length, 10 mm.

Male.—Front, cheeks, and clypeus conspicuously masked under mass of dense white appressed hair. Front with minute punctures much more numerous than primaries on lower half, and extending upward to level of ocellus. Cheek as wide as diameter of an antennal fossa. Clypeus with its median extension bidentate, and without an impunctate apical band; lateral carina short and moderately folded, barely overhanging the lateral pit for a short distance. Mandible without cusp.

Dorsum of pronotum with transverse carina complete and high; anterior portion with punctures moderate, largely of second-degree density, secondaries almost lacking. Mesepisternum on outer disc with primary punctures separated by distances equal to their diameter, interspaces densely beset with minute punctures, and if unrubbed, a mat of fine appressed white hairs. Legs brownish black, piceous in some aspects. Tegula black, polished, without a marginal groove. Wings with radial cell in its lateral extension greatly exceeding the second cubital.

First tergum with a high, arcuate transverse carina, posterior to which the dorsum is polished and impunctate except for widely scattered obsolete primary punctures and the preapical band, which is one to two punctures wide, shallowly impressed, the punctures being well separated. First sternum with lateral groove continuous to the escutcheon, the polished disc with a few subobsolete primary punctures but without minute punctures. Intermediate terga with coarse, subobsolete punctures concentrated both in front of and behind a nearly impunctate intermediate area. Second sternum without a polished impunctate anteromedial callosity. Sixth sternum without a denticle.

Length, 8.5 mm.

Redescribed from type, a female labeled "Cuba, type no. 579.1" and the male paratype labeled "Cuba, no. 579.2" (A.N.S.P.). There are also in the type series a female paratype, a male paratype, and several identified males labeled "Cuba."

In addition we have examined the following material, all of which was collected in Cuba. In the Harvard Museum of Comparative Zoology: Cienfuegos, 2 ♀♀, August and September 1930; Cienfuegos, 7 ♂♂ (Dow); Santa Clara, 2 ♂♂ (Dow). In the U. S. National Museum: Camaguey, 1 ♀, June 19, 1950; 1 ♂, November 3, 1929; Caymas, 1 ♀, May 25 (Swartz); El Cano, Habana, 1 ♂, February 4, 1932 (Bruner); 1 ♂, March 16, 1932 (Bruner and Otero); L. de Ariguanabo, 1 ♂, October 15, 1922 (Bruner and Ballou); Nagua, Oriente, 1 ♀, July 7, 1922 (Bruner and Ballou); Santiago de las Vegas, 1 ♀, January 15, 1916 (Hutson); 1 ♂, 1921 (Acuna); 1 ♀, December 1, 1923 (Bruner); 1 ♂, May 19, 1924 (Bruner); 1 ♂, October 1, and 1 ♂, October 11, 1934 (Bruner); Upper Yara Valley, 2 ♂♂, October 28, 1918 (Scaramuzza).

It seems remarkable that in Cuba, males that have the elongated radial cell and prominent transverse carina of the first tergite are associated with females that have no groove on the hind basitarsus, whereas in the eastern United States such males are invariably associated with females having the grooved hind basitarsus.

We are unable to separate from males of *argentipes* the males from Santa Clara, Cuba, collected with females of *dowi*. Some of the males mentioned above differ considerably from the type of *argentipes* in having less conspicuous appressed white hair on the front, cheeks, and mesepisternum, and in having the radial cell not greatly exceeding the second cubital cell in lateral extent. However, even in the small series studied there seems to be intergradation.

At or near the beginning of this century there were several references in the literature to *argentipes*, and some of these recorded it from islands in the West Indies other than Cuba. These are not reliable since most of the diagnostic characters of *Tiphia* species have been discovered since 1918.

Tiphia dowi new species

Female.—Front with primaries largely of first-degree density up to level of lowest ocellus except for a median impunctate vitta. Clypeus with its median extension subtruncate, and scarcely as long as the diameter of an antennal fossa; lateral carina rather short, but thinly folded, and below the cheeks, overhanging a rather deep lateral pit.

Hind tibia on inner surface with the margin of the bare area perceptibly elevated above the adjacent setulose area; sensorium and adjacent area black; major calcarium only slightly expanded just before the middle. Hind basitarsus 5.0 times as long as middle width, and with a short, very shallow groove on inner face. Wing usually with an apically inclined spur at the outer anterior angle of the second cubital cell; posterior margin of second cubital cell with the preapical section usually about twice the length of the apical section.

Posterior slope of propodeum only shallowly and sparsely sculptured except for several short transverse rugae bordering the lateral carina. Dorsum of abdomen conspicuously polished. First tergum with preapical band consisting of an even line of discrete punctures, one puncture wide, not impressed. Terga 2, 3, and 4 with conspicuous intermediate impunctate areas, caudad of which are bands of coarse, deep punctures; apices medially broadly impunctate. First sternum with a well-developed lateral groove continued into the shallowly punctate area immediately caudad of the escutcheon; apical sulcus absent or vestigial. Pygidium coarsely rugoso-punctate on basal half; impunctate portion shagreened in the wrinkled area, polished apically.

Length, 9 to 10 mm.

Male.—Unknown.

Type.—Female, labeled "San Jose Trinidad Mts. Santa Clara, Cuba, August 30, 1930, Richard Dow" (M.C.Z.).

Included in the type series are three female paratypes from the same locality collected by Richard Dow, August 27, 1930 (M.C.Z.). This species has numerous small differences which separate it from *argentipes*. The presence of a groove on the hind basitarsus presumably places it in an entirely different group.

A MONOGRAPH ON FOOD SELECTION IN ORTHOPTERA[1,2,3]

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[1] Portions of the included material are modified from a dissertation submitted in 1956 in partial fulfillment of the requirements for the degree of Doctor of Philosophy, University of Michigan.

[2] Contribution No. 38 from the Department of Biology, Wayne State University, Detroit 2, Michigan.

[3] Part of the considerable expenses of publication of this report were born by the American Entomological Society and part by the National Science Foundation under grant NSF-G19357.

HISTORY OF STUDY

The grasshoppers, locusts, grouse locusts, katydids, crickets, camel and cave crickets, praying mantids, walking-sticks, and cockroaches composing the insect order Orthoptera (*sens. lat.*)[4] are relatively large, readily observed, and often economically important. It is not surprising that they have been the subject of many scientific investigations. The foregoing would lead one to conclude that the group is very well understood. Such is not the case, for most research on the group has been devoted to a few rather restricted phases of the insects' biology, particularly their taxonomy and control, leaving prominent gaps in our knowledge of the group as a whole. Surprisingly, this is notably true of the insects' feeding behavior.

Riley (1878) emphasized the nearly omnivorous food-habits of *Melanoplus spretus* in outbreak populations but also showed that this species, even under these abnormal conditions, feeds differentially and, hence, is not truly omnivorous. Most entomologists, who are unfamiliar with the latter findings, regard the Orthoptera as omnivorous or, at least, highly unselective. This point-of-view has been most fully championed by Urquhart (1941). He found little, if any, differential feeding among thirteen species of grasshoppers and katydids. Ball (1936), Isely (1938, 1941, 1946), and others, to the contrary, demonstrated conclusively that differential feeding does take place in Orthoptera, particularly Acrididae.

The accumulation of feeding records has been carried on for years by entomologists. Most of the records pertaining to Orthoptera, particularly the older ones, are based on scattered, often inaccurate observations on a few species of economic interest. Furthermore, these observations were frequently made on insects under abnormal outbreak conditions. These isolated field observations are profusely distributed throughout various taxonomic, ecologic, and economic journals. More extensive studies containing feeding records, all on acridids, were published by, among others, Agrawal (1955), Ball (1936), Clark (1948), Golding

[4] The term *Orthoptera,* as here used loosely, includes insects belonging to the orders Orthoptera and Dermaptera, both of which are customarily studied by orthopterists.

(1935, 1937, 1940), Joyce (1952), and Williams (1954). Of especial merit is the work of Anderson and Wright (1952), who obtained feeding records of 36 species of rangeland grasshoppers.

Various types of differential feeding tests have been used to study food selection in Orthoptera. Savin (1927), working on *Acheta*, fed many kinds of foods to her caged crickets and used the time required for complete consumption of a given food as an index of preference for that food. Unfortunately, she studied a small, variable number of closely confined crickets. Furthermore, the time required for consumption is not necessarily an indication of preference value; the time required for consumption of coarse-textured foods is generally much greater than that for fine-textured ones, though their preference value may be identical.

Roonwal (1953) placed several different foods in a cage inhabited by many starved *Schistocerca gregaria;* after a 15-minute wait he took the number of individuals eating each plant as an index of preference for that particular food, and he compared it with the number eating *Heliotropium,* which was selected as the standard. His technique may be open to some criticism because his method of maintaining random distribution of grasshoppers may result in alteration of behavior, because starved grasshoppers are not likely to be very selective in their choice of food, and because the number of feeding individuals may be subject to counting error.

Chapman (1957) cut leaves of test grasses into small pieces, which he mixed thoroughly and placed in a heap in the center of his cages. By so doing, he hoped to overcome the tendency toward unequal presentation of foods. His locusts were exposed to these foods for one hour, after which the contents of the animals' digestive tracts were analyzed. Chapman's interesting method, though it answered his needs, may be somewhat objectionable in that cut grasses, particularly those cut into small pieces, desiccate very rapidly with consequent modification of their preference value. Furthermore, the feeding response elicited through this method of presentation of food-plants must be greatly altered from that under more natural conditions.

Other investigators have estimated food preferences by the degree of damage inflicted on several different plants during a comparatively long exposure to feeding Orthoptera. Among them are Pfadt (1949), who conducted cage experiments on *Melanoplus b. bilituratus;* Isely (1938, 1946), who performed insectary experiments on many species of Acrididae and Tettigoniidae; Clark (1948), who confined his acridines to cages enclosing parts of their natural habitats; and Duck (1944), who tested the preferences of *Schistocerca obscura* caged in nature.

Husain, Mathur, and Roonwal (1946) used cotton as a standard with which to compare other foods. They placed the same number of grasshoppers in each of two cages exposed to similar conditions. A fresh twig of the plant under trial was then placed in the experimental cage and one of the cotton plant in the control cage. The amount of leaf eaten was determined after 24 hours and, on this basis, preferences estimated.

Rau (1945) baited a number of cockroach traps, each with its own type of food. He then used the number of cockroaches caught in the traps as an index of preferences for the different foods.

Joyce (1952) estimated the preference value of various plants in terms of the number of times each was accepted per 100 presentations. As he admitted, however, data thus derived are perhaps not as refined as those from other techniques.

The analysis of crop contents has recently come into acceptance as a tool with which to study food selection of Orthoptera. Lüstner (1914) and Crumb, Eide, and Bonn (1941) examined large numbers of crops of the earwig *Forficula* to gain information on its feeding habits, and, among others, Beall (1932), Boldyrev (1928), Bennett (1904), Brindley (1918), Chapman (1957), Davidson (1943), Forbes (1905), Fulton (1915), Grassé (1922), Grinfeld (1957), Gurney (1953), Hubbell (1936), Jordan (1909), Monti (1902), Rémy (1931), Terry (1905), and Thierolf (1928), also using this method, obtained valuable data on the species they treated. Especially worthy of note is the work of Isely and Alexander (1949), who briefly described the mechanics and significance of crop analysis in the study of feeding behavior of insects, and that of Mulkern and Anderson (1959),

who described a method of crop analysis which greatly facilitates identification of such materials.

Except for the study of Boldyrev (1928) and of Verdcourt (1947), who analyzed the fecula of, respectively, *Bradyporus* and *Tetrix*, there appears to be no feeding information in the literature of Orthoptera based on analysis of fecal materials.

While zoologists have long appreciated the value of using structural characteristics of animals as keys to the diagnosis of their habits, this indirect method of studying food selection has been ignored, for the most part, by entomologists. The sole feature frequently so-used by orthopterists is the armature of the legs; for example, the powerful armature of the legs of mantids and sagines has rightfully been taken as indicative of predacious habits. Further correlations between the structural characteristics of Orthoptera and their food-habits were anticipated, to a degree, by Smith (1892). Isely (1944) was the first, however, to show the close correlation between the mandibular structure of acridids and tettigoniids and their feeding habits. Gangwere (1960a, 1962, 1962a) revealed correlations between the food-habits of Orthoptera and the structure of their mouthparts and digestive tract.

In light of the above brief review of the literature it would appear that the orthopterist has at his disposal a number of excellent techniques for the study of food selection, which should have enabled him to have reached, at this time, a reasonably accurate understanding of the food-habits of the major groups and of some of the species, particularly economic ones, of the order. However, there are gaps. Most feeding studies have dealt with a few species belonging to one or two related groups of Orthoptera. There has not been a study embracing a sizable portion of an orthopteran fauna, though Isely's superb researches were directed toward that goal when they were terminated by his death. Certain rangeland faunas, which necessarily are restricted to a very limited assortment of food-plants, are, of course, partial exceptions. Neither has there been a study emphasizing availability, a factor of great importance in food selection, nor has there been an attempt at an analysis of the major factors which influence food selection, though a number of partial

analyses have appeared. Finally, no studies have been made specifically pertaining to food selection in Orthoptera inhabiting a region of the eastern United States. Such a study would be valuable for comparison with Isely's work in Texas. A comparison of this nature is needed because it is here concluded that the whole question of food selection requires restudy for each different orthopteran fauna and its associated flora.

OUTLINE OF PRESENT STUDY

Field observations on feeding Orthoptera were made in southern Michigan during the 1953 through 1955 and the 1957 through 1959 seasons. During this time a total of 300 feeding records were amassed for 48 species of Orthoptera and allies. The field observations were carried out at stations in Nichol's Arboretum, a 90-acre tract belonging to the University of Michigan; at the E. S. George Reserve, a 1,268-acre wildlife preserve belonging to the Museum of Zoology, University of Michigan; and at numerous other localities in the Ann Arbor, Michigan, area. Many of these stations were visited only once or twice, but 34 were visited regularly.

Differential feeding tests were carried out repeatedly on 32 species of Michigan Orthoptera, most of them being investigated in this manner for the first time. These tests are unusual in several respects: (1) an especially large number of species belonging to the non-omnivorous groups of Michigan Orthoptera was tested; (2) an unusually large number of food-plants was used, for most species of Orthoptera were exposed to 30 or more species of plants, from which information a fairly comprehensive idea of the total range of food preference of each was obtained; (3) most Orthoptera were offered repeatedly at least 10 of the most consistently available foods, and, thus, an accurate estimate of the relative preference value of the more abundant plants of the insects' habitats was obtained.

The crop materials of 58 species and the fecal materials of 43 species of Michigan Orthoptera were analyzed. In addition, the mouthparts of 64 species were studied under the microscope, during the course of which it was posssible to classify them in terms of their structural adaptations for feeding.

METHODS

OBSERVATION OF INDIVIDUALS FEEDING IN NATURAL HABITATS

A most successful way to observe the feeding activities of Orthoptera consists of going to a selected spot and sitting there quietly for 15 to 30 minutes or so until the effect of the disturbance ceases and the insects resume movement. This technique was the one used to amass most of the feeding records presented in this study. The more conventional method of seeking feeding individuals while walking slowly through a community was also used but was not as successful. Most of the observations were made with the naked eye. Occasionally, tripod-mounted 7 × 35 Bushnell binocular field glasses were used, but it was found difficult to keep the actively moving insects in focus. The feeding individuals were collected, whenever possible, together with their food-plants, for a laboratory check of the field identification.[5] Field observations on the nocturnally active species were made with the aid of a head-lamp operated by a 6-volt battery.

UTILIZATION OF DIFFERENTIAL FEEDING TESTS

The techniques used in the differential feeding tests combine some of the features of both Isely's and Roonwal's methods, while perhaps avoiding certain faults common to experimental methods for measuring preferences. For a given food-plant they involved: (1) evaluation of the comparative degree of damage inflicted by feeding over an extended period of time; (2) counts at regular intervals of the number of individuals feeding. Care was exercised that the Orthoptera used in the experiments were not unduly crowded, starved, or disturbed during observation.

The maintenance techniques and equipment used in this study were described previously (Gangwere, 1960), but a discussion of their salient features is appropriate here. A total of 10 to 20 individuals of each species was confined in individual cylindrical screen cages 12 to 18 inches high and 9 inches in diameter. The

[5] The methods used in the determination of all species, both orthopteran and plant, are reviewed in the Appendix.

cages were aligned on a narrow bench parallel to and 3 feet from the southern windows of a large laboratory room with windows on two sides, where the animals received direct sunlight during 5 or 6 hours of the day. The windows were left open to keep the temperature and humidity as close as possible to that prevailing outdoors.

Food-plants to be tested were clipped in the field and their stems thrust immediately into water-filled 5- or 8-ounce jars. A group of 6 to 12 plant species was assembled from the above jars to be placed in each test cage in the laboratory. In most cases, only a single plant of each forb species was used in a cage, but grasses and sedges were tied in small bunches composed of many plants. All damaged or torn leaves and flowers were carefully removed, and the total bundle of plants was placed in a water-filled tumbler. Paper was then wadded around the plant stems, which served to hold them upright in the containers and to prevent the insects from falling into the water and drowning. Finally, the tumblers were placed in the cages. Generally, no drinking water was provided because the insects proved able to get all they needed from the fresh vegetation (Gangwere, 1960b).

Fresh foods were made available to the insects during early afternoon, and, in order to count the number of individuals feeding on each food-plant, the cages were observed at hourly intervals until late night. Counts were continued during the next morning and afternoon, and the position of the plants in each cage was changed several times. During the second night, the plants were removed from the cages, and the amount of damage inflicted on each was noted and recorded. The relative preference value of each plant species was then estimated on the basis of degree of damage and number of feeding records. Sometimes the food fragments found on the floor of the cage were helpful in making this determination.

Only non-omnivorous Orthoptera were studied in the above manner, for omnivorous ones were considered so unselective as to be unproductive in tests of this type.

ANALYSIS OF CROP CONTENTS AND FECAL MATERIALS

The data from crop analysis were obtained from 4 or 5 specimens of each species studied. These individuals were collected, killed immediately in cyanide, and stored in 80% alcohol. The crops were removed by pulling the head of each animal from its body, the crop and sometimes the entire digestive tract pulling free with the head. Once exposed, the crop was slit and its contents emptied onto a microscope slide for examination in alcohol. Especially interesting preparations were made permanent with polyvinyl alcohol. Some balsam slide mounts of rhaphidophorine crop materials, prepared by T. H. Hubbell, were also studied.

Each analysis of fecal materials was based on a minimum of 50 fecula per species, of which 5 or more were examined in detail on slides. The rest were studied, dry and intact, in a more cursory fashion. To collect fecula, orthopterans were caught and placed immediately in clean, empty jars from which the pellets were gathered after 6 hours. The fecula were stored dry until analysis.

STUDY OF STRUCTURAL ADAPTATIONS OF MOUTHPARTS

The mouthparts used in this investigation were dissected from 3 or more alcohol-preserved specimens of each species studied. They were usually examined in alcohol with the aid of a binocular dissecting microscope, but permanent microscope slides were prepared of the mouthparts of smaller species. The heavily sclerotized mandibles of some species were also examined as dry preparations, in which prominences and excavations are more clearly visible than in wet ones.

DISCUSSION OF RESULTS

The results of this study are summarized in a series of tables and graphs presented in the final section of this paper. The results of the feeding observations are presented in Table I and Graph I; those of the differential feeding tests in Table II and Graph II; those of the analysis of crop contents and fecal materials in Graph III; and those of the analyses of mouthpart

adaptations in Table III. More meaningful presentation of the results is given in the following discussion sections. Here, certain results of especial significance are reviewed in the light of pertinent information from the literature.

REVIEW OF TECHNIQUES USED IN STUDIES OF FOOD SELECTION

Several methods have been used in the past in the study of food selection in Orthoptera: (1) the observation of plants frequented by species of Orthoptera; (2) the analysis of food debris found in or near dwellings of Orthoptera; (3) the observation of individuals feeding in natural habitats; (4) the utilization of differential feeding tests; (5) the analysis of crop contents and fecal materials; (6) the study of structural adaptations for feeding.

The first of these methods, the *observation of plants frequented by species,* is of very limited value in the study of food selection, for, while a species is perhaps somewhat more likely to be found on a preferred than on an unpreferred food-plant, its choice of perch is often fortuitous. The unreliability of this technique is best illustrated by various carnivorous species which frequent certain plants to feed on their insect faunas but not on the plants themselves. Monophagous and oligophagous species, however, may be exceptions, for they are seldom found except on their food-plants, which sometimes comprise much of the available vegetable materials of their habitat; apparent examples of such species, as indicated by the literature, include *Aeoloplides* on *Atriplex, Sarcobatus,* and certain other chenopodiaceous plants (Wallace, 1955); *Aularches miliaris* on *Calotropis* (Chopard, 1938); *Bootettix* on *Larrea* (Ball, 1936; Rehn, 1944); *Clematodes larreae* on *Larrea* (Ball *et al,* 1942; Scudder, 1900) and probably on *Acacia* (Rehn: personal communication); *Derycoris tibialis* on *Anabasis aphylla* (Uvarov, 1928); *Graeffea coccophaga* on coconut palms (Chopard, 1938); *Insara covilleae* on *Larrea* (Rehn and Hebard, 1914; Rehn: personal communication); *Inscudderia taxodii* on cypress (Caudell, 1921; Chopard, 1938; Hebard, 1925); *I. strigata* probably on *Hypericum fasciculatum* (Hebard, 1925); *Melanoplus davisi* and *M. quercicola* on oaks

(Hebard, 1918); *Diapheromera covilleae* on *Larrea* (Rehn and Hebard, 1909); *Oecanthus pini* on *Pinus* and *Larix* (Beutenmüller, 1894; Cantrall, 1943); *Tropidolophus formosus* on *Malvastrum coccineum* (Ball, 1936); and *Schistocerca ceratiola* on *Ceratiola ericoides* (Hubbell and Walker, 1928).

No strictly monophagous or even oligophagous species are included among those investigated in this study. Consequently, the method was not used.

The second method, the *analysis of food debris found in or near dwellings* of Orthoptera, is even less generally applicable than the first because very few species have habits lending themselves to study in this manner. Furthermore, data derived in this fashion are of poor quality. The Indian crickets *Brachytrypes* (Ghosh, 1912) and *Gymnogryllus* (Singh, 1952) have been studied in the above manner. The method was not used.

The third method for the study of food selection, the *observation of individuals feeding in natural habitats,* is both difficult and time consuming to use because Orthoptera are discontinuous feeders (Gangwere, 1958) and wary, hence, difficult to approach sufficiently close for accurate observation. Nevertheless, field observation of feeding is an excellent method to obtain direct, reliable information on several aspects of the animals' feeding behavior, including their food selection, feeding periodicity, and food consumption under natural conditions. This technique may also be used as an aid in planning and interpreting experiments. Thus, a few nights' observation of *Neoconocephalus ensiger,* for example, will disclose its " seed "-feeding habits. Without such knowledge, one might perform countless differential feeding tests and yet be unsuccessful in revealing this cone-head's food-habits. Isely (1944) believed this method somewhat unreliable because he felt that field evidence of food choices by grassphoppers is difficult to obtain and easily misinterpreted. To the contrary, the present author's several years of experience with the method have convinced him of the excellence of the technique, an impression apparently shared by Anderson and Wright (1952) and others who have used it extensively.

The method contributed much of the data here presented.

The fourth method, the *utilization of differential feeding tests,* enables one to determine readily and accurately what insects eat by preference when the factor of availability is cancelled out. Beyond simply revealing food preferences, the tests offer, through the use of an acceptance-rejection ratio [6] or a similar index, a quantitative method of expressing the relative attractiveness of foods. Consequently, one may predict with some certainty the relative attractiveness of two food-plants not previously tested together. This prediction is accomplished through a comparison of their acceptance-rejection ratios or by comparing each with other plants previously tested with each. During the course of differential feeding tests, observations on food-seeking and food-taking behavior, on food consumption, and on feeding periodicity may be made.

Unfortunately, the use of the tests is not without difficulties. The results vary somewhat from test to test. This variability is expected because the rankings are based on criteria which are sometimes subjective; because the testing process is somewhat laborious, and, hence, most foods are necessarily incompletely tested; and because many factors relative to both food and feeders influence food selection. Thus, animals caged together are likely to behave abnormally in their artificial environment. This tendency is most pronounced under conditions of limited space, amount, and choice of food; for more valid results crowding must be minimized. Caged grasshoppers may also congregate toward one side of their cage by reason of their phototaxis, resulting in increased feeding on plants in that part of the cage; the alternative foods constantly must be shifted with respect to the light source to counteract this tendency. Still other behavioral factors may have to be taken into account. Not only must the foods be equally accessible, but they must be fresh and equally abundant. Because it is difficult to find plants not already mutilated by feeding, one must grow his own or resort to the use of partly damaged ones from which all injured portions have been removed. After a given exposure to the feeders, each food must be examined carefully to determine its relative damage. Such evaluations are often difficult and subjective, especially when the

[6] See foot-note 18.

plants are small, highly branched, and wilted or curled. The evaluation between totally different types of plants such as fine grasses and large, coarse-leaved forbs is especially difficult.

Differential feeding tests were conducted in this study because of the previously listed advantages they offer, which far outweigh any disadvantages.

The fifth method for the study of food selection, the *analysis of crop contents and fecal materials*, can yield both qualitative and quantitative data. The samples are easily obtained and analyzed, and they furnish information based on natural conditions. Of the two types of materials, crop contents and fecula, the former yield better data, but the latter are more readily collected and analyzed. The insects do not have to be killed to obtain fecula, and the pellets can be collected over a period of time from a single individual having access to a variety of foods. The incidence of empty crops among individuals collected at known times of the day provides information on feeding periodicity.

Data derived from these analyses are, unfortunately, much less precise and reliable than those from the observation of feeding individuals and from differential feeding tests. This may be attributed, in part, to the fact that the materials of which they are composed have been subjected to the digestive processes of the animal and, hence, are broken and much-altered. It also results, in part, from the fact that crops taken from two specimens of a highly omnivorous species may contain completely different materials, though the insects were captured within a few feet of one another.

Analyses of crop contents and fecal materials may disclose animal remains, largely fragments of insects, including their body sclerites, femora, tibiae, tarsi, setae, spines, scales (Lepidoptera), mandibles, wings, antennae, compound eyes, head capsules, cast skins, etc., most of which usually cannot be determined to order. The analyses more commonly reveal plant materials of various types, including leaf fragments of woody plants, forbs, grasses, and mosses. Floral parts such as the pappus and ray flowers of composites, perianths of other dicots, flowers and fruits of grasses, pollen of monocots and dicots, and

spores of fungi and ferns may be distinguished. Hyphae, individual vascular and epidermal cells, and plant hairs and fibers often appear. Sometimes the contents are mineral in nature. Such remains are almost entirely sand grains, the presence of which is usually correlated with scavenger feeding habits.

The method was used successfully in this study.

The last method for the study of food selection, the *study of structural adaptations for feeding,* is limited in application. However, when used with discretion, it can be informative, for it is possible to make a reasonable guess about the gross nature of the food-habits of a species by examination of its mouthparts. Isely (1944) was the first orthopterist to make extensive use of the method. His researches were limited to the mandibles, which he found may vary with different kinds of foods and are, therefore, diagnostic of food-habits. The present author has extended this idea to other parts of the insect, for he has discovered that all mouthparts and even the alimentary canal possess variably developed structural adaptive features.

The present paper is concerned wholly with food selection. A detailed consideration of structural adaptations is beyond its scope but has been presented elsewhere (Isely, 1944; Gangwere, 1960a, 1962, 1962a). However, the following brief summary of mandibular adaptations taken from Gangwere (1962) is pertinent. The mandibles of carnivorous Orthoptera have hook-like, somewhat sharp dentes or " teeth," which are reminiscent of the fangs of certain predacious mammals. Seminivores or " seed "-feeders have hook-like, blunt dentes. Omnivores and forbivores have numerous, short, rather sharp dentes of fairly uniform length. Dendrophagous species, which are feeders on leaves of woody plants, have sturdy, low dentes, which may be fused into one or several continuous ridges. Graminivores or grass-feeders have dentes fused into many parallel grinding ridges, which remind one of the tooth pattern of ungulates.

The forte of this method is the ease with which it may be used, but conclusions based on this evidence alone are not reliable. The mandibles of cockroaches and of grouse locusts are, for example, of omnivorous type. The former are truly omnivorous species, while the latter, though scavengers, have a

marked preference for mosses and other lower plants. The mandibles of forbivorous and of dendrophagous species of Phaneropterinae are similar, though their food-habits differ. The mandibles of *Atlanticus*, a shield-backed katydid, indicate strongly developed carnivorous habits, but the insect is as much an omnivore as a carnivore. Mandibles are subject to wear. Consequently, those of senescent individuals may be misleading. One must conclude that information from the study of structural adaptations for feeding, though of value in supplementing other data, cannot be used alone in studies on food selection.

Therefore, the method was purely a supplementary one in the present study.

REVIEW OF FEEDING IN THE GROUPS AND SPECIES OF ORTHOPTERA

It is meaningless to talk about the food-habits of Orthoptera because feeding in this order is so diversified as to defy description. A more meaningful discussion is obtained by considering the food-habits of individual families and subfamilies of the order. The following section is such a description. It stresses food selection but also includes remarks on other aspects of feeding behavior. Admittedly, the conclusions here outlined are sometimes sketchy, tentative, and subject to debate. Nevertheless, they reflect the author's impression of the food-habits of southeastern Michigan Orthoptera, which are then reviewed and expanded in light of material from the voluminous literature dealing with the subject. A considerable portion of the pertinent literature is used in the case of some groups, but in others in which the literature is more extensive only selected references are given.

The following discussion is summarized in Table IV. This table is based on a majority of the species of each group and ignores variations of food-habit which may occur in certain species.

Dermaptera: Earwigs [7]

Doru, the only earwig studied, has mandibles of omnivorous type. This nocturnally active insect was not seen feeding, but analyses of its crop contents and fecal materials showed that it may feed almost exclusively on grass pollen, though it takes some animal materials. Many individuals were placed in a cage containing ground beef and *Carex lacustris,* other sedges, and flowering plants of *Potentilla fruticosa, Solidago canadensis,* and *Spiraea alba.* The earwigs ate the meat but also spent much time visiting the stamens and pistils of *S. alba;* whether they actually ate the later is uncertain. The other plants were untouched.

The literature on feeding in Dermaptera is very extensive. In consequence, a somewhat limited number of salient references is given below.

Morse (1920) found *Prolabia* and *Euborellia* living in a slaughterhouse basement, where they were eating decomposing animal matter. Other genera have been recorded feeding on dead fish, insects, and greasy paper. Some appear to be predacious. *Labidura* feeds extensively on larvae of the cotton worm in Egypt (Clausen, 1940). Terry (1905) recorded *Chelisoches* eating living leafhoppers and other insects, and Risbec (1935) recorded additional prey of this insect. Berland (1929) described the way in which *Euborellia* penetrates rotten apples to devour larvae located in the core. *Anisolabis* and *Sphingolabis* were noted as predators of fruit flies in Hawaii and were found to be so voracious that they killed more fly larvae than they consumed (Marucci, 1955).

Strenger (1950) found that the well-known *Forficula auricularia* is not a predator but is an omnivore which prefers the stamens and pistils of flowers and also eats leaves, dead insects, and living, defenseless small animals. Other authors have emphasized its predatory propensities. Thus, it was said to eat voraciously springtails of the genus *Smynthurus* (Maclagan, 1932) and to pursue larvae of *Gracilaria syringella* on lilac (Pussard, 1926). Other records of predation by *Forficula* were listed by

[7] The Dermaptera, though an order separate from the Orthoptera, are customarily studied by orthopterists, which justifies their inclusion in this account.

De Coursey (1951), Dimmock (1884), Frohawk (1940), Hawker-Smith (1943), and McLeod and Chant (1952). Predation on aphids, as noted by Voukassovitch (1924), probably also relates to this species of earwig. Goe (1925) first claimed that *Forficula* eats only soft-bodied insects such as aphids, but later (1928) admitted that it does eat vegetable materials. Crumb, Eide, and Bonn's study (1941) revealed that it may often be a scavenger; that it consumes more vegetable than animal food, the latter of which may be taken dead or alive in the form of small insects; and that it shows no really marked preferences in its plant feedings, though lower plants, particularly mosses and lichens, are more often eaten than are higher ones. Fulton (1924) found that dead and injured earwigs of *F. auricularia* are sometimes eaten by individuals of their own species but maintained that predation is not usually carried to the point of cannibalism. Later (1927), he stated that, notwithstanding its preference for animal materials, plants form the greatest part of its diet in nature.

In summary, it is probable that most earwigs are omnivorous, but many have a tendency toward carnivorous habits, and some are highly voracious predators. The bulk of their diet in nature is, however, usually vegetable because of the comparative scarcity of suitable animal materials. *Doru,* a Michigan earwig, appears to eat pollen and some animal materials, but it, too, may be omnivorous, though having a preference for proteinaceous foods.

Blattidae: Cockroaches

Most cockroaches in this country, like *Parcoblatta,* are geophilous, nocturnal forms which live under leaves, bark, and woodland debris and seldom wander into dwellings of man. One may turn to Hebard (1917) for a discussion of the habits of several of these wild species. Many genera, however, are domestic and cosmopolitan. Examples of the latter are *Blatta, Blattella,* and *Periplaneta,* on which innumerable studies have been made, the classical one of which is Miall and Denny (1886). The domestic species live in the dwellings and other establishments of man and are especially common in restaurants, hos-

pitals, bakeries, grocery stores, kitchens, and other places where there is organic debris, which serves as food, and considerable humidity.

Aside from the many cockroaches observed feeding on oatmeal trails (Gangwere, 1958), these insects were seen but twice feeding in nature, once on fresh rodent dung and once on a small *Crataegus* pome. Analyses of crop contents and fecal materials showed the organic debris and insect sclerites characteristic of scavengers. Preference studies were not undertaken for such obviously omnivorous animals, though a number of individuals of *Blattella* and *Parcoblatta* and some of the exotic *Byrsotria* were reared successfully in cages containing lettuce, oatmeal flakes, and bran flakes. The mouthparts of blattids are of omnivorous type.

The literature on feeding in Blattidae is very extensive. In consequence, a somewhat limited number of salient references is given below.

Tepper (1900) observed the Blattidae feeding on caterpillars and softbodied insects and considered them eminently carnivorous and cannibalistic. Green (1909) recorded predation by *Periplaneta australasiae* on a struggling winged termite. *Parcoblatta pensylvanica* was recorded by Blatchley (1920) eating dead *Tenebrio* grubs and by Rau (1940a) eating a larva of *Polistes*. Cockroaches were said by Thiagarajan (1939) to eat small earwigs of the genus *Euborellia*. The highly carnivorous *Blatta orientalis* is known to be a control for the bed bug (Pettit and McDaniel, 1918; and other authors). The cannibalistic habits of cockroaches as described by Howard and Marlatt (1902) were verified by Gould and Deay (1938) and by Rau (1940), who found that dead and injured individuals are eaten by their mates.

Though it would appear that living vegetation is less frequently taken than is dead, Morse (1920) stated that in greenhouses *Periplaneta australasiae* attacks the tender tips of the aerial roots of orchids, and Skinner (1905) described it as injurious to foliage and flowers of orchids, roses, and carnations. The nymphs of *Pycnoscelus*, another well-known greenhouse pest, were said by Caudell (1925) and by Zappe (1918) to bur-

row in the soil, where they eat bark from the stems of young roses, Easter lilies, and poinsettias. Fulton (1930) recorded *Parcoblatta* feeding on an apple, a record which parallels one obtained during the present study.

Cockroaches are fond of secretions and wastes of animals. Records illustrative of this point are one of an individual of *Parcoblatta uhleriana* observed during this study feeding on rodent feces, one of *Periplaneta australasiae* feeding on excrement (Blatchley, 1920), one of *Pycnoscelus surinamensis* eating chicken feces (Schwabe, 1949), and one of several cockroaches imbibing mucous from the nostrils of a sleeping human (Rau, 1940). *Cariblatta* may also feed regularly on excrement (Wolcott, 1923). Additional records of this type were listed in a very detailed report by Roth and Willis (1957).

The domestic cockroaches have food-habits of such familiarity to the entomologist that little need be said about them. It is sufficient to note that they are fond of almost any edible substance, either fresh or decayed, animal or vegetable in origin, including cardboard, paste-board, wallpaper, glue, paste, clothing, wastes of various types, water color paints, book bindings, leather, hair, and foodstuffs, particularly soft items rich in starchy materials. Among these foods are many not normally eaten by insects. In fact, as reported by Gier (1947), one individual of *Periplaneta americana* lived for 101 days on a diet of distilled water and filter-paper.

The curious *Cryptocercus*, an inhabitant of the Appalachian and Pacific Coast areas, dwells in soggy sapwood galleries within chestnut, pine, oak, and other logs, feeding on wood, the cellulose of which it cannot digest except through the agency of its symbiotic flagellates (Cleveland, 1934).

In summary, the range of foods eaten by cockroaches is astonishingly great, which justifies their reputation as omnivores *par excellence*. Nevertheless, even cockroaches manifest certain preferences. Dead plant and animal materials appear to be preferred to living ones, though both are eaten by these nocturnal insects. Animal foods are less often eaten than are plant materials probably because of their lesser availability but not because of preference. Domestic species exhibit a strong preference for amylaceous foods but eat a vast array of materials,

many of which are not usually food for insects. *Cryptocercus* has food-habits like those of termites.

Mantidae: Praying Mantids

Detailed observation of mantids was impossible because of the scarcity of the introduced *Tenodera aridifolia sinensis,* the Michigan species. The few observations made during this study are based on examination of the mouthparts of preserved specimens and of the feeding process in a few caged nymphs and adults. Fortunately, the literature on these well-known predacious insects is large and fairly complete.

Most mantids are phytophilous insects color-adapted to blend with their surroundings. They remain motionless on the vegetation and await the approach of prey, but when hungry they may stealthily stalk their prey. In contrast, several xerophilous forms, *Eremiaphila* (Uvarov, 1921), *Litaneutria* (Roberts, 1937), and *Yersiniops* (Ball *et al,* 1942; Rehn and Hebard, 1909), are adapted for running on the ground and actively seeking prey, a necessity because of the severe selective conditions under which they live, and *Metallyticus* [8] is reported to run rapidly over limbs while searching under bark for cockroaches, on which it feeds exclusively.

The mouthparts of mantids, especially their fang-like mandibles, are beautifully adapted for carnivorous habits, but the well-known modifications of their fore legs for capturing prey are perhaps even more remarkable. The coxae are greatly elongated, and the femora and tibiae fold together to make a pincer armed with spines for piercing and holding captured insects. Other adaptations are their marked ability to move their head in various directions and their acute vision, which enable them to watch prey before capturing it.

Many observers, including Breland (1941), Gurney (1951), Mathur (1934), Williams and Buxton (1916), and Rau and Rau (1913), have written about the feeding behavior of mantids, and the report of Beier and Heikertinger (1952) is especially complete; thus, the behavior reported below does little more than

[8] Citation apparently erroneously attributed to Wood-Mason, 1878 (Chopard, 1938).

corroborate the results of others. Mantids pounce on their prey and capture it with their fore legs. Sometimes they commence feeding on the abdomen of the prey, and sometimes they first immobilize it by biting through the nape of its neck and then feed on its head before eating the rest of the body. The prey is eaten alive, and only the hard parts, *e.g.*, wings, legs, and jaws, are left unconsumed. Any edible parts accidentally dropped are ignored. It was reported by Ball *et al* (1942), Caudell (1902), Didlake (1926), and others that they may catch a second insect before eating the first, holding one in each spiny fore leg. This latter behavior was not observed.

Mantids refuse non-living and non-moving animals and animal materials, though Roeder (1936) and Gurney (1951) found that they accept uncooked meat thrust to them on a stick or forceps. With regard to prey, however, their food preferences are said to be negligible. Certain butterflies (Chopard, 1938), moths (Beebe and Kenedy, 1957), bugs (Barlow, 1895), and ants (Gurney, 1951) are unattractive to mantids. Breland (1941) reported that only a few kinds of insects are able to escape mantids, among them being certain highly sclerotized, hence, armored beetles. Didlake (1926) described a differential feeding correlated with growth and increase in size. She found that small insects, such as leafhoppers, fruit flies, and geometrid caterpillars, are eaten by young nymphal mantids; larger leafhoppers, larger flies, and nymphal grasshoppers by second- and third-instar nymphs; and almost any large insect, including hairy caterpillars, furry moths, stink bugs, wasps, cockroaches, grasshoppers, and mealworms, by adult mantids. A similar progression of prey was noted in *Gongylus* (Williams, 1904), *Mantis* (Rollinat, 1926), and *Tenodera* (Hadden, 1927).

The tendency of female mantids to cannibalize males mating with them has been noted in both entomological and popular literature. An early report of this behavior is that of Howard (1886). It is probably a less sensational but more realistic view that mantids eat virtually any insect close enough to be reached and weak enough to be overpowered, their own species included; thus, when copulation brings male and female together, the

smaller, weaker male is often sacrificed. Rummel (1926) remained almost alone in denying the common occurrence of cannibalism during coition of mantids.

Even vertebrates may not be immune to attack by mantids. There appear in the literature many sketchy, largely unverified reports of these voracious predators attacking various small species of vertebrates. Somewhat better substantiated are records of an attack on a shrew (Teale, 1944), a mouse (Wymbs, 1939), a hummingbird (Laurent, 1933), another small bird (Burmeister, 1864), a frog (Frank, 1930; Rau and Rau, 1913), and a lizard (Mourque, 1909). Two additional records, the eating of a protesting tree frog and of a lizard, were listed by Beier (1933). A mantid was also recorded killing, though not eating, a small sunbird (Brown, 1899).

In summary, the Mantidae are the only wholly carnivorous members of the Orthoptera observed in this study. Their foods consist entirely of prey, usually insects, which they capture by means of modified fore legs and eat with mouthparts of carnivorous type. They sometimes stalk their prey but usually lie in wait for it to move close enough for capture. They have few, if any, food preferences, capturing virtually any insect which they can reach and overpower, members of their own species included.

Phasmidae: Walking-Sticks

Mouthpart studies, analyses of crop contents and fecal materials, feeding records, and differential feeding tests suggest that the slow-moving, nocturnal, phytophilous Michigan phasmid *Diapheromera femorata* is restricted to eating the leaves of certain deciduous woody plants. All feeding records were on leaves of woody plants, especially *Quercus,* though one case of nibbling on *Lespedeza,* a forb, was observed. This record must, however, represent aberrant feeding behavior. Laboratory preference tests show that *D. femorata* is highly selective, but not oligophagous, as some workers have suggested; thus, *Quercus velutina* and *Rubus* were found to be highly preferred; *Cornus stolonifera, Tilia,* and *Ulmus,* at best, moderately acceptable; and most other woody plants and all forbs and grasses completely unacceptable.

The marked preference of *D. femorata* for *Rubus* is interesting. This food-plant has not been recorded previously as a food of the

phasmid, though comparatively lesser choices such as *Hamamelis, Prunus,* and *Tilia* frequently have been so listed. The failure of previous workers to observe feeding on the highly preferred *Rubus* can probably be explained by the arboreal habits of the phasmid adults, which, because of their apparent negative geotaxis, are found in the tree tops, where they feed largely on oaks. The only opportunity of adults to eat *Rubus* is on occasions when they fall from their lofty perches, as they sometimes do. The nymphs of *D. femorata* lack the negative geotaxis and occur near the ground, where the available foods are quite different. The above view accords with statements by Graham (1937) and by Williams (1907), who maintained that young nymphs of this walking-stick have feeding habits unlike those of older nymphs and adults. Older nymphs probably feed on saplings of the preferred trees and shrubs, including *Rubus*. More work is needed.

Diapheromera femorata is usually listed as a species of some economic importance, feeding on oaks and cherry, sometimes on witch hazel, as well as on other woody plants. Graham (1937), for example, observed one outbreak in which *D. femorata* first defoliated black oak and then descended to eat sweet fern and witch hazel but left untouched white oak, red maple, aspen, and conifers. Those observations accord with laboratory and field data obtained during the present study.

Phasmids other than *D. femorata,* especially adult individuals, are also phytophilous and largely restricted to feeding on leaves of certain woody plants, as illustrated by *Anisomorpha buprestoides* (Hetrick, 1949), *Aplopus mayeri* (Strohecker, 1952), *Megaphasma dentricus* (Craighead, 1950), *Podacanthus wilkinsoni* (Froggatt, 1905), and *Phyllium bioculatum* (Leigh, 1909; St. Quintin, 1907), and various other species. Such must also be the case with most European species, which, according to Chopard (1938), are encountered in a small number of shrubs belonging to the Leguminosae and Rosaceae. This dendrophagous behavior sometimes reaches the point of monophagy, as with *Graeffea coccophaga* (Chopard, 1938).

Some species choose plants other than woody ones. *Diapheromera covilleae* apparently feeds exclusively on *Larrea* (Rehn

and Hebard, 1909; Rehn: personal communication). Körting (1934) listed the non-woody genera *Begonia, Euphorbia, Galinsoga,* and *Tradescantia* as possible food-plants of *Carausius morosus* but in his experiments proved this insect's preference for certain woody plants. Davis (1923) implied, but did not state, that *Diapheromera blatchleyi atlantica* feeds on goldenrods and related plants; *Pseudosermyle* was noted by Ball *et al* (1942) to feed on grasses, as were the young of *Bacillus* (Thomson, 1882); and *D. velii* and *D. persimilis* probably have non-dendrophagous food-habits because they occur in abundance in prairie and plains environments in which trees and shrubs are wholly absent (Cantrall: personal communication; Hebard, 1931).

No species of Phasmidae live as predators, though some may show a tendency toward cannibalism. Certain stick-insects are known to eat their cast skins (Severin and Severin, 1911; St. Quintin, 1907) and, under starvation, to nibble on one anothers' appendages (Beier, 1934; Roth, 1917). To the contrary, Grimpe (1921) attributed the damaged appendages of *Phyllium bioculatum* to necrosis.

In summary, most phasmids are characterized by considerable specificity of food-habit, sometimes to the point of oligophagy or monophagy. The dendrophagous habits of *D. femorata,* which shows great preference for the leaves of *Quercus velutina, Rubus,* and certain other deciduous woody plants, are perhaps typical of this family, but it would appear that there are some grass- and forb-feeders in this nocturnal group.

Acrididae, Acridinae: Slant-Faced Locusts

All species of Acridinae examined in this study have mandibles of the graminivorous type. The mandibles of *Syrbula admirabilis* and of *Pseudopomala brachyptera* are typical of this condition, whereas those of *Chloealtis conspersa* show a slight tendency toward the herbivorous type. This herbivorous tendency is somewhat stronger in *Orphulella speciosa* and in *Chorthippus longicornis.*

On occasions when the author observed acridines feeding in nature, they ate grasses, except once when *Chloealtis* was seen

eating dried leaves of wild strawberry (*Fragaria*). The crop contents and fecal materials of *Chorthippus, Pseudopomala,* and *Syrbula* yielded only grasses; those of *Chloealtis* and *Orphulella* also included a minor element of forbs.

The outcome of the differential feeding tests was uniform. True grasses were almost always accepted by the above five species; sedges, rushes, and the horsetail *Equisetum arvense* were often accepted; forbs and woody plants were seldom accepted and then only to the extent of being nibbled.

The last statement should be qualified. Brooks (1958) described *Psoloessa* as graminivorous but found that it also readily eats the forb *Phlox hoodii.* Phipps (1930) recorded the feeding of *Chorthippus longicornis* on blueberry leaves and, under starvation pressure, on lettuce; Richards and Waloff (1954) discovered that the related European species *C. parallelus* prefers the grass *Holcus* but occasionally eats *Trifolium* and certain other forbs; and *Chloealtis conspersa* was found, though infrequently, by Phipps and by the present author to accept forbs. The above records correlate with the fact that *Chorthippus* and *Chloealtis* are two of the three acridines mentioned above as having slight modification of their mandibles in the direction of the herbivorous adaptation. The third one, *Orphulella,* like *Chloealtis,* was found to have dicot leaf materials in its crop contents. It would appear that *Orphulella* may also belong in this occasional forb-feeding group.

The above information indicates that the species of Acridinae studied are strongly but variably graminivorous. *Pseudopomala* and *Syrbula,* both of which have strongly graminivorous-type mandibles, are exclusively grass-feeders, while *Chloealtis, Chorthippus,* and *Orphulella* are grass-feeders which occasionally or rarely vary their diet with forbs. The graminivorous, phytophilous, diurnal habits of the above Michigan species are probably typical of the subfamily, for *Acrida* (Hafez and Ibrahim, 1958), *Amphitornus* (Isely, 1938), *Chorthippus parallelus* (Richards and Waloff, 1954), *Dichromorpha* (Isely, 1946), *Eritettix* (Ball *et al,* 1942), *Mermiria* (Isely, 1938), and *Syrbula fuscovittata* (Isely, 1946), a number of slant-faces with known food-habits, are also graminivorous. While it has not been definitely established, it is probable that most acridines, including the above,

starve in the absence of grasses. This latter would appear to be true of *Syrbula admirabilis,* starved individuals of which were here found to reject lettuce, one of the forbs most attractive to Orthoptera, including Acrididae, but it is not true of *Ageneotettix,* which, according to Isely (1944), turns to forbs under starvation pressure.

In contrast to the typical acridines exemplified by the above species are certain anomalous genera of the southwestern United States. Several of them, if not all, possess mandibles of forbivorous adaptation, and they are known to be forbivores which feed on one or several species of plants. The habits of these forbivorous genera have been discussed as follows: *Acrolophitus* by Isely (1937, 1938, 1944), Criddle (1933), and Anderson and Wright (1952); *Bootettix* by Isely (1944) and Rehn and Hebard (1909); *Goniatron* by Chopard (1938) and Rehn (1923); *Ligurotettix* by Ball (1936), Ball *et al* (1942), and Rehn (1923); and *Pedioscirtetes* by Ball *et al* (1942).

In summary, the Acridinae, except the anomalous genera above, constitute a group of graminivorous, diurnally active Acrididae. They select freely from among the many grasses and sedges occurring in their communities. Some of them rarely or occasionally accept forbs and, in minor amount, even leaves of woody plants, but most species probably starve rather than feed exclusively on such plants.

Acrididae, Oedipodinae: Band-Winged Locusts [9]

The mouthparts of the Oedipodinae examined in this study were of graminivorous type in *Arphia p. pseudonietana, A. sulphurea,*[10] *Dissosteira carolina,* and *Encoptolophus s. sordidus* and of herbivorous type in *Camnula pellucida, Chortophaga viridifasciata, Pardalophora apiculata, P. haldemanii, Spharagemon b. bolli,* and *S. collare.* These mouthpart data correlate positively with feeding records obtained for the species, though *Dis-*

[9] Rehn and Grant (1960) recently transferred the genera of the Oedipodinae to the Acridinae. This classification has not been adopted here because food selection in the two groups is quite different. Hence, it is convenient, if not correct, to retain the older classification.

[10] A detailed analysis of the feeding behavior of this insect is now in preparation by the author. It includes a total of 27 feeding records not here recorded.

sosteira, which also took some forb and moss material, and *Camnula,* which took only grasses, are partial exceptions.

The differential feeding tests revealed considerable variation between the food-habits of these strongly diurnal species, even those within the same genus. Notwithstanding this variation, the traditionally diverse oedipodines have, as indicated by the tests, two fairly distinct patterns of food selection, which are in harmony with their mandibular structure. Those species with mandibles of graminivorous type seldom accept forbs, and two of them, *Arphia p. pseudonietana* and *Encoptolophus s. sordidus,* are as closely restricted to grasses as are acridines, whereas those with mandibles of herbivorous type frequently accept forbs, though they have a preference for grasses. It is interesting to note that *A. p. pseudonietana* was listed by Criddle (1933) and by Isely (1944) as a mixed-feeder, an impression in direct contradiction to evidence from the present study.

Oedipodines accept grasses as readily as do acridines, though they are not restricted to them (Graph II). Additional proof is furnished by unpublished cage experiments by Gangwere on *Arphia sulphurea* and *Chortophaga viridifasciata,* in which individuals of these species survived for extended periods when restricted to forbs. Much the same can be said for *Encoptolophus s. sordidus,* which, according to Fry (1927), can produce viable eggs when restricted to lettuce.

On the basis of the available literature, it appears that most oedipodines, like the species observed in this study, are strongly diurnal in their feeding and other activities and either geophilous or phytophilous. The above-listed patterns of food selection, *viz.,* graminivory and herbivory, must also be fairly typical, for they are characteristic of a number of band-wings with known food-habits. Examples are *Arphia xanthoptera, Chortophaga australior, Trimerotropis verruculatus,* and *T. maritima interior* (Carothers, 1923), *Encoptolophus s. costalis, E. subgracilis,* and *Spharagemon collare cristatum* (Isely, 1938), and *Hippiscus ocelote* (Ball *et al,* 1942), which are graminivorous or largely graminivorous; and *Trimerotropis citrina* and *T. pistrinaria* (Isely, 1938), which are largely herbivorous.

There are, however, several interesting dietary variations in the group. Analyses of crop contents and fecal materials revealed a predominance of grass fragments, while the quantity of dicot materials was insignificant, but the analyses also produced, in certain species, a small amount of grass pollen. This content is not surprising, for pollen grains are a normal but minor component of the diet of all oedipodines and, in fact, of all grass-feeding acridids. *Spharagemon collare,* a species noted in the laboratory for its propensity to feed on grass spikelets, had a somewhat higher proportion of pollen in its crop contents than did any of the others.

Insect fragments were found in the crop contents of *Encoptolophus* and *Spharagemon collare.* This observation confirms a tendency toward carnivorous behavior in oedipodines noted by Coquillet (1886), who saw an individual of *Trimerotropis pseudofasciata* feeding in nature on the body of another grasshopper. This tendency has also been noted by the present author, who found that caged oedipodines and cyrtacanthacridines sometimes eat weak, dying, or newly dead individuals of their own and other species. While it is not certain whether the insect fragments found within the crops were a result of scavenging or of predation, the former is certainly the more likely.

The crops of several species of Michigan oedipodines also held traces of moss leaves. In fact, half of the crop contents of *Dissosteira* was composed of such material. Both *Dissosteira* and *Spharagemon b. bolli* were observed eating moss in nature. It has not been reported previously that oedipodines other than saxicolous mountain- or desert-dwellers, such as *Circotettix r. rabula* (Ball *et al,* 1942), *Heliastus benjamini* (Ball, 1936), or *Scirtetica ritensis* (Ball, 1936), feed on mosses, algae, fungi, or lichens. The author believes that mosses and lichens may well be normal components in the diet of bare-ground Orthoptera, *e.g., Arphia p. pseudonietana, Dissosteira carolina,* and *Spharagemon collare.* The above evidence lends support to this contention.

In summary, the diet of the Oedipodinae, a diurnally active group, is less uniform than that of the Acridinae. Some species are restricted or virtually restricted to grasses and sedges, while

others accept forbs as readily as they do grasses, and still others, particularly certain species of the western United States, are reported to accept lower plants. As a group, however, oedipodines are largely graminivorous, accepting grasses at least as readily as do acridines, though they are not restricted to them. They may vary this diet with considerable forb material and with minor amounts of animal foods and lower plants.

Acrididae, Cyrtacanthacridinae: Spine-Breasted Locusts

The Cyrtacanthacridinae is a diurnally active, largely phytophilous group of grasshoppers. The Michigan species of this structurally and behaviorally heterogeneous group have diverse mouthparts which fit into six adaptive patterns constituting a graded series, with intermediates, ranging from graminivorous through herbivorous to forbivorous. The graminivorous adaptation apparently is not as prevalent in the Cyrtacanthacridinae as it is in the Oedipodinae and especially in the Acridinae. Only one species, *Leptysma marginicollis,* has mouthparts of this type, while seven have those of forbivorous type. Furthermore, of the eight species having the intermediate herbivorous mandibles, only one of them, *Phoetaliotes nebrascensis,* tends toward the graminivorous type, as opposed to four favoring the forbivorous.

As shown by the analyses of crop contents and fecal materials, the differential feeding tests, and especially the feeding records, forb-feeding is favored in the Cyrtacanthacridinae. In fact, this is the only subfamily of Michigan Acrididae in which the preference for forbs is greater than that for grasses. This tendency is not marked, however, for, notwithstanding some variation between species, the relative acceptability of forbs is not much greater than that of grasses; which, in turn, is not much greater than that of woody plants (Graph II).

In general, the above food-habits are correlated with mandibular form, but the relative degree of forb-feeding does not always increase proportionately to the degree of forbivorous modification of the mandibles. This latter may indicate that herbivorous and forbivorous mandibles, which are not dissimilar, serve almost equally well in forb-feeding. It may also indicate, in this case, an artificial separation of mandibular types. More investigation is needed.

There are considerable differences in food-habits among the species of Cyrtacanthacridinae. Some species, for example, *Leptysma marginicollis,* appear to be almost wholly graminivorous and probably cannot subsist in the absence of grasses, though Ball (1936) found that the latter eats cat-tail; other species, like *Melanoplus plebejus,* are graminivorous but may subsist for a time on forbs alone (Isely, 1944); others, such as *Campylacantha olivacea* and *Hesperotettix viridis* (Isely, 1938), as well as *Melanoplus keeleri luridus* (present study), are strongly forbivorous, accepting grasses but probably being unable to subsist exclusively on them; others, like *Melanoplus confusus,* are herbivorous and, hence, intermediate between the two extremes (present study), though Isely (1938) found that *M. confusus* requires forbs for survival; still others are dendrophagous, feeding on the leaves of woody plants.

Examples of the dendrophagous Cyrtacanthacridinae include *Anacridium aegyptium* (Johnston, 1924), *Appalachia arcana* Hubbell and Cantrall, 1938; Rehn and Rehn, 1936), *Aptenopedes aptera* (Davis, 1914), *Dendrotettix quercus* (Davis, 1912; Rehn and Rehn, 1938), *Melanoplus davisi* and *M. quercicola* (Hebard, 1918), and *Schistocerca damnifica* (Isely, 1944) and *S. lineata* (present study; Hubbell, 1960), all of which feed on the foliage of various broad-leaved trees and shrubs. *Melanoplus punctulatus* apparently prefers conifers but also eats leaves of deciduous trees (Cantrall, 1943). *Melanoplus splendidus* eats conifers (Ball *et al,* 1942). Some of these dendrophagous species also accept forbs. *Schistocerca lineata,* as indicated by the present investigation, accepts forbs and is quite partial to *Lespedeza.* A relative, *S. obscura,* eats various plants ranging from cotton and wheat to elm, especially the last (Duck, 1944). The Japanese species *Prumna uzume* includes several woody plants among its foods, though it selects largely from among forbs (Katô, 1940).

The polyphagy prevailing in the Cyrtacanthacridinae may account for the fact that a large proportion of the grasshoppers of economic importance in this country belongs in this subfamily. Many spine-breasts, especially when their populations are in

outbreak proportions, attack almost indiscriminately grains, garden crops, trees, native grasses, forbs, dung, dead animal materials, and are even known to take cloth, rake handles, and other materials not normally food of grasshoppers and may be cannibalistic. The magnitude of their depredations has been described frequently. Two reports, that of Riley (1878) and that of Villamor (1914), are especially descriptive. Nevertheless, not all cyrtacanthacridines are polyphagous. *Aeoloplides* and *Melanoplus davisi* and *M. quercicola* are said to be oligophagous, the former on members of the Chenopodiaceae (Ball, 1936; Wallace, 1955), and the latter on oaks (Hebard, 1918). *Schistocerca ceratiola* is monophagous on *Ceratiola ericoides* (Hubbell and Walker, 1928). Other examples of monophagy and oligophagy in the Cyrtacanthacridinae have been reported.

There appears to be a carnivorous tendency in the Cyrtacanthacridinae. The author found that twenty-five per cent of the crop contents of *Melanoplus confusus* was of insect remains, and Grassé (1922), during analyses of the intestinal contents of *Orthacanthacris aegyptia,* discovered a minor amount of insect remains. The present author noted, as did Abbott (1944), several instances of cage spine-breasts feeding on weakened, injured, or dying members of their own species. Furthermore, a nymphal *Melanoplus* sp. was here observed feeding in nature on the remains of a *M. b. bilituratus* crushed by an automobile, and an individual of *M. confusus* was discovered feeding on the dried remains of a cricket of the genus *Acheta.* James (1932), who observed *M. bivittatus,* also found this genus cannibalistic in nature. Additional evidence of a carnivorous tendency is furnished by observations on spine-breasts in serious outbreak populations. As noted above, they feed on an astonishingly wide assortment of materials, including animal ones.

Cannibalism in acridids has been linked with water shortages by some authors (Uvarov, 1931), but others have attributed it largely to lack of food (Husain, Mathur, and Roonwal, 1946). It seems more likely that both lack of water and lack of food, as well as a possible innate craving for animal foods, are factors in this behavior.

The Cyrtacanthacridinae, like certain Oedipodinae examined in this study, occasionally may feed on lower plants. Two species, *Melanoplus b. bilituratus* and *Schistocerca lineata,* were observed feeding in nature on leaves of moss plants, and one species, *M. f. -r. femur-rubrum,* was found to have a small proportion of moss leaves in its crop contents. Nevertheless, in view of the paucity of such records and particularly in view of the habitat selection of most spine-breasts, which regularly are exposed to more acceptable foods, it would appear that feeding on mosses and other lower plants is not important in the subfamily, except in instances of outbreak populations.

The literature on feeding in Cyrtacanthacridinae is very extensive. In consequence, it was necessary to use in the above discussion a limited number of salient references.

In summary, the Cyrtacanthacridinae is a heterogeneous, diurnally active group with heterogeneous food-habits. Its members are largely forbivorous but select very widely from among forbs, grasses, and woody plants. Not all species manifest such latitude, however, for some are restricted to one or another of the food groups and starve in the absence of this food. This restriction seldom extends to the point of oligophagy or monophagy. Occasionally spine-breasts are somewhat carnivorous.

Tetrigidae: Grouse Locusts

The studies carried out on this group, though not intensive, were sufficient to reveal the general nature of their food-habits. They included an examination of mouthparts, observations during rearing, and analyses of crop contents and fecal materials. The mouthparts of the three species examined, *Tetrix ornata, T. subulata,* and *Tettigidea l. lateralis,* were of omnivorous type.

Food	Highly Preferred	Moderately Preferred	Taken Occasionally	Not Taken
Hypnum (a moss)	X			
Mnium (a moss)	X			
Various sprouting seedlings		X		
Muck			X	
Soggy decayed wood			X	
Bran flakes			X	
Leaf litter			X	
Lettuce				X [11]
Oat flakes				X

[11] At a later time when only lettuce was provided they ate it readily.

The above cage experiment, in which ten *Tetrix subulata* and *Tettigidea l. lateralis* were exposed to various foods, provides additional evidence of omnivorous habits.

The data obtained by analyses of crop contents and fecal materials were variable but along anticipated lines. Particles of moss leaves and organic debris, composed largely of algae, molds, and decaying vegetation, were predominate; grass seedlings composed most of the remainder of the contents; sand grains, spores, and dicot leaf materials were also present in equal, small amounts.

These observations accord generally with the few published records. Verdcourt (1947), also through analyses of fecal materials, found the diet of *Tetrix* to be composed largely of the leaves of *Hypnum* and allied mosses, the remainder being composed of stem, rhizoids, and secondary protonema of mosses, together with a very small quantity of epidermal tissues from the leaves of higher plants. He was unable to confirm the presence of algae. Hancock (1898, 1902) observed grouse locusts feeding on various substances, including black muck, decomposing soil, organic debris, algae, lichens, molds, mosses, and seedlings of grasses, sedges, and dicotyledonous plants. Cantrall (1943) on several occasions watched insects of this group as they ate heavy black muck and mosses. Somes (1914) recorded them eating tender stems of young grain and clover.

In summary, grouse locusts are apparently omnivorous-herbivorous. Most of their feeding is on decaying vegetable substances and lower plants, *e.g.*, algae, molds, lichens, and especially mosses, but they also feed on sprouts of both monocotyledonous and dicotyledonous plants. They are quite partial to black muck. They do not seem to feed on animal materials.

Gryllacrididae, Rhaphidophorinae: Camel and Cave Crickets

A few field observations were made on the feeding activities of individuals of several species of *Ceuthophilus*, a genus of completely nocturnal, geophilous camel crickets. They ate animal remains, leaf mold, and fungi. Many were also seen feeding on oatmeal trails (Gangwere, 1958). Individuals caged in the lab-

oratory ate lettuce and flakes of bran and oats. Differential feeding tests were not attempted for such obviously omnivorous organisms. Organic debris, leaf materials of dicotyledonous plants, and spores predominated in the crop contents and fecal materials; insect remains were common components; and a few sand grains, hyphae, and grass leaves were also present. The mandibles of *Ceuthophilus* are of modified omnivorous type, an adaptation which, though different from that of cockroaches and most other orthopteran scavengers, is well-suited for such a varied diet.

Hubbell (1936) found that peanut butter is especially preferred by caged *Ceuthophilus,* but molasses, cheese, butter, jam, fruits, meat, and dead insects are also avidly eaten, while grass and other kinds of green vegetable materials are untouched, except in the absence of more acceptable food. He found insect fragments, decayed vegetation, spores, hyphae, and pollen in the crop contents. Hubbell's caged insects were not predacious, nor did they indulge in cannibalism, except when the victims were soft and helpless during molting. Turner (1915), to the contrary, said that adult females of *Ceuthophilus* possibly eat the males during copulation.

There are, in the literature, additional records pertaining to *Ceuthophilus* and related genera. Monti (1902) pointed out the important role which fecal materials of man and his domestic animals play in the diet of certain cellar-dwelling Ceuthophili; Banta (1907) found that *Ceuthophilus* feeds on organic matter and once watched an individual eat the decaying body of a mouse, as well as bait cheese; Townsend (1893) even reported *Ceuthophilus* feeding on curtains and clothes hung out to dry; Muehlberger (1938) noted that his caged *Troglophilus* ate moss but refused small insects; and two authors, Popenoe (1922) and Thomas (1939), mentioned damage inflicted on mushrooms by, respectively, *Pristoceuthophilus* and *Ceuthophilus.*

Apparently, many rhaphidophorines, like *Ceuthophilus,* are not normally predacious nor cannibalistic but are scavengers which confine their animal diet to the weak or dead. Nevertheless, there is in the subfamily a number of powerful, aggressive carnivores as prone to attack their own kind as others. Smith (1920) recorded *Udeopsylla robusta* feeding on May beetles, grasshop-

pers, and various other insects. Wünn (1909) found the introduced greenhouse cricket *Tachycines asynamorous* a rapacious predator, as did Boettger (1950), though the latter also discovered that this species eats vegetable materials but is unable to mature on them.

The cave-dwelling Ceuthophili, according to Bailey (1928), are more restricted to a scavenger diet than are the others. They probably eat bat dung, molds, dead insects and cave mice, and organic materials they encounter during their wanderings. Such food sources either originate there or are washed in from above. In contrast, individuals of *Macropathus,* a New Zealand cave-dweller, were shown by Richards (1954) to be omnivores which feed on leaves, grass, remains of dead insects, and sometimes living prey, some of which they must obtain in wanderings outside their cave retreats. This latter type of feeding behavior of cave-dwellers must not be uncommon.

In summary, the rhaphidophorines, which are perhaps typified by the nocturnal *Ceuthophilus,* are highly omnivorous, the variety of their diet being second to none, except that of cockroaches and perhaps field crickets. They are attracted to spores, molds, hyphae, pollen, and dead plant materials but are also fond of animal substances, largely newly dead insects and dung. A few species are aggressive predators.

Tettigonidae, Phaneropterinae: Bush and Round-Headed Katydids

Analyses of feeding records and of crop contents and fecal materials of some Michigan phaneropterines show that, in order of decreasing preference, forb leaves, forb flowers, and leaves of woody plants are accepted as food. The differential feeding tests confirm these results, revealing that forbs are consistently accepted, woody plants frequently accepted, and grasses seldom accepted by these insects of nocturnal, phytophilous habit (Graph II). Such food-habits are in harmony with the mandibles of forbivorous type [12] possessed by virtually all phaneropterines examined.

[12] Isely (1944) terms such mandibles *florivorous-forbivorous.*

The foliage of *Impatiens,* along with that of certain other succulent forbs, is greatly favored by Michigan phaneropterines. The flowers and leaves of *Solidago canadensis* and certain other composites are also taken frequently because they are both preferred and abundant in the insects' natural habitats. The leaves of various vines and shrubs, particularly *Vitis* and *Rhamnus,* proved to be more acceptable than are those of trees. The leaves of saplings of the latter are more often taken than are those of mature plants. The more succulent, tender parts of all foodplants are preferred over the coarser, older parts.

On the basis of the above, it would appear that the Michigan species of Phaneropterinae eat leaves and flowers of various forbs and leaves of woody plants and usually reject grasses and sedges. The latter checks with the little information available on these species and on *Amblycorypha p. parvipennis* (Isely, 1944) and *Arethaea grallator* (Isely, 1941), two species not here studied. One can conclude, therefore, that the Phaneropterinae is a generally phytophagous group, though, contrary to statements by Chopard (1938) and Ramme (1932), it may not be exclusively phytophagous.

Some insect sclerites were discovered in the crop contents of *Amblycorypha rotundifolia.* There are three records which perhaps bear on this surprising discovery. La Baume cited the European species *Barbitistes* as a possible predator on larvae of the moth *Liparis monacha,* though this relationship was doubted by Chopard (1938); Urquhart (1938) noted two instances of cannibalism in *Scudderia pistillata;* and *Microcentrum retinerve* was reported predacious on certain beetles (Griffith, 1882). Notwithstanding these records, one must conclude, on the basis of present information, that any carnivorous behavior, at least in Michigan species, represents somewhat aberrant feeding. The few insect fragments found in the crop of *Amblycorypha* must be considered atypical and doubtlessly the result of scavenging, not of predation.

Urquhart's work presents an anomaly. In 1938 he tested the laboratory feeding of *Scudderia pistillata* and found that this species has a marked preference for poplar and grass. In 1941 he tested individuals of *Scudderia texensis* and *S. f. furcata* and

found that his caged insects accepted any of the grasses and sedges he offered them, as well as lettuce and other cultivated forbs. In contrast, the tests made during the present investigation showed, time after time, that grasses and sedges are quite unacceptable as foods, though they may be eaten lightly or nibbled, particularly during times of food shortages. Urquhart's data are so completely unrepresentative of the normal feeding behavior of phaneropterines that it is likely that his results may have been biased owing to starvation pressure. Evidence of the latter is furnished by the fact that he found *Scudderia pistillata* cannibalistic, a tendency in some starved orthopterans.

The food-habits of *Scudderia septentrionalis,* a seldom-encountered arboreal species, are largely unknown. The author was able to obtain several individuals for experimentation from the oak-hickory woods of the E. S. George Reserve and the Ann Arbor area. During two tests they ate fronds of *Pteridium* and heads of *Rudbeckia,* the former being preferred, and they nibbled several plants, particularly shrubs. These plants can scarcely be the insects' normal foods, for they grow in the shrub-forb stratum of the woods, where the animals do not live. Early mortality of the katydids helped confirm this impression. The species is probably dendrophagous, feeding on some woody plant not included in the two tests.

Microcentrum rhombifolium, according to Isely (1944), differs from most other phaneropterines in having mandibles tending toward the dendrophagous type. It eats woody plants rather than herbs, which coincides with its arboreal habits. There is, however, some evidence which indicates that this genus is not exclusively dendrophagous. Blatchley (1920) reported that members of this species can be reared on succulent forbs, such as lettuce, though such individuals are less hardy and shorter-lived than those having access to the foliage of woody plants. A relative, *M. retinerve,* has been reported predacious on certain beetles (Griffith, 1882), and another, *M. triangulatum,* is known to feed on the leaves of sweet potato and castor bean (Wolcott, 1923).

In summary, the phaneropterines, katydids of nocturnal habit, are almost completely phytophagous, probably eating, in order of decreasing preference, forb leaves, forb flowers, and leaves of

woody plants, while usually rejecting grasses and sedges. A few species are, however, more dendrophagous than forbivorous and show appropriate modification of their mandibular form.

Tettigoniidae, Copiphorinae: Cone-Headed Katydids

Only a single species of copiphorine, the nocturnal *Neoconocephalus ensiger,* was included in the present study, but it was investigated rather thoroughly. All individuals seen feeding in nature were, with two exceptions, eating grass " seeds " or grains. Hubbell (unpublished field notes) recorded a related species, *N. triops,* feeding on fruiting heads of the grass *Sorghastrum;* Davis (1889) another relative, *N. exiliscanorus,* those of *Spartina;* and Davis (1914) a related genus, *Pyrgocorypha,* those of an unnamed grass. The mouthparts of *N. ensiger* proved to be of seminivorous type, especially adapted for grass " seeds." The analyses of crop contents and fecal materials confirmed the " seed "-eating habits of the species, for the only trace of any other food consisted of a few insect remains.

In the differential feeding tests on *N. ensiger,* as in those performed by Isely (1944) on *N. robustus crepitans,* grass spikelets were consistently accepted and leaves of grasses were consistently rejected, as were leaves and flowers of forbs (Graph II). In fact, *N. ensiger* accepted the grains of virtually every true grass offered it, except those of *Elymus,* and it proved to be particularly fond of those of *Andropogon,* a plains grass which occurs in abundance in many of the animal's habitations in southeastern Michigan. It accepted commercial parakeet seed and also demonstrated a moderate preference for the fruits of several sedges common in the marsh situations in which it sometimes lives. During periods of food shortage caged individuals hesitantly accepted lettuce and grapes, presumably attracted by their high water content, but because of their mouthpart structure they were unable to feed efficiently. Starvation pressure may perhaps force them into predation. Smith (1892) observed them eating living individuals of the meadow grasshopper *Conocephalus,* and, in the present study, a small amount of the fecal materials subjected to analysis was of animal origin.

Not all copiphorines are "seed"-eaters or, at least, as restricted to this diet as is *Neoconocephalus ensiger*. Gowdey (1923) found that *N. maxillosus*, a Jamaican species, feeds on the leaves of sugar cane, and Davis (1912a) recorded the southern species *Belocephalus sabalis* as a palmetto-feeder, which gnaws the tough leaves with its powerful jaws. In contrast, a close relative, *B. subapterus*, probably has food-habits more like those of *N. ensiger* (Hubbell: unpublished field notes).

In summary, the food-habits of the Michigan species *Neoconocephalus ensiger* probably typify those of the Copiphorinae, the subfamily of nocturnally active insects to which it belongs. It is virtually restricted to grains or "seeds" of grasses, among which it selects very widely, but its diet includes some fruits of sedges. Animal foods are not a normal component of the diet but, when necessary and available, possibly may be taken at infrequent intervals. Other parts of grasses and sedges and all parts of forbs and woody plants are consistently rejected. Certain copiphorines depart from the above, eating the tough leaves of various plants.

Tettigoniidae, Conocephalinae: Meadow Grasshoppers

The mouthparts of conocephalines, insects of incompletely nocturnal habits, show an admixture of the forbivorous, seminivorous, and carnivorous adaptations. There is concomitant variability in their food selection. The feeding records obtained show that the conocephalines of southeastern Michigan prefer flowers of forbs and fruits of grasses, sedges, and rushes, but sometimes capture prey and also eat leaves of grasses, sedges, and forbs. The above correlates generally with data supplied by Isely and Alexander (1949), except for their impression that feeding on the leaves of grasses and forbs is negligible. The differential feeding tests carried out yielded data supporting the above field observations, for they showed that meadow grasshoppers have great preference for grasses and certain forbs and moderate preference for sedges, with reproductive parts of these food-plants being favored over vegetative ones. They also revealed, on the basis of Graph II, that grasses and forbs are almost equally acceptable, while both are preferred to leaves of woody plants.

Evidence from the analysis of crop contents and fecal materials presents a slightly different picture. These materials consisted primarily of dicot leaves and insect sclerites but included some flowers, fruits, and pollen of grasses and dicots. This discrepancy in proportions may be resolved if one holds that conditions in the experimental cages did not give the insects, which are characterized by great latitude in feeding behavior, sufficient opportunity to exhibit fully their broad range of preference. It may also be explained by an inadequate sampling of crops.

It is probable, on the basis of information from this study, that carnivory is well developed in the Conocephalinae, though the animals are not completely insectivorous, as Chopard (1938) thought they might be. *Conocephalus brevipennis* was observed feeding on a freshly killed, adult deerfly and on a dead, undetermined fly larva, and *C. strictus* was observed preying on an ant, a mosquito, and an undetermined insect. Other species of *Conocephalus* are known to be predacious. The Hawaiian species *C. saltator,* according to Swezey (1905), Illingworth (1929), and Clausen (1940), may be the principal agent in the natural control of mealy-bugs. Members of the genus *Orchelimum* are predacious. The author's caged *Orchelimum* ate several kinds of living animals, including nymphal *Scudderia,* reduviid bugs, coccinellid beetles, and individuals of the lygaeid bug *Oncopeltus fasciatus.* Blatchley (1920), Balduf (1943), and Knowlton and Roberts (1943) also observed predation in this genus of meadow grasshoppers. The present author's caged *Orchelimum,* as well as *Conocephalus,* were found to be cannibalistic, continually reducing their numbers by eating weaker members of their own species. The former genus, *Orchelimum,* had previously been noted as cannibalistic (Hancock, 1904; Metcalf and Colby, 1930). There is probably little choice of prey in the Conocephalinae, as in most other orthopteran predators, except that based on size and inability of the prey to escape or to defend itself.

Conocephalines exhibit distinct preferences, even though they select widely from among many different kinds of foods. They prefer living to dead materials, whether plant or animal. Animal foods are probably preferred over plant foods, but they are less often taken because of their lesser availability. Among foodplants, grasses, sedges, and forbs are taken, in general order of

decreasing preference, but species differ markedly in the relative preference they show for these foods. Reproductive parts of plants are preferred over vegetative ones.

In summary, the Conocephalinae, a group of incompletely nocturnal insects, feed on a very wide range of foods. They are predacious, but a large part of their diet in nature is necessarily composed of the flowers and leaves of certain forbs and the fruits of many grasses and sedges.

Tettigoniidae, Decticinae: Shield-Backed Katydids

Observations were made on the food-habits of but one species of decticine, the incompletely nocturnal *Atlanticus testaceus,*[13] during this study. Its mandibles are of carnivorous type. Insect fragments predominated in the crop contents and fecula, but a small amount of dicot leaf material and organic debris was also present. Caged individuals ate pieces of meat, fruits of blueberries (*Vaccinium*) and strawberries (*Fragaria*), lettuce, flakes of oats and bran, a variety of species of forbs, including both leaves and flowers, and leaves of grasses and woody plants. They showed greatest preference for the meat and fruit. They were also predacious on various flies, beetles, bugs, and grasshoppers. These observations accord with published accounts. Cantrall (1943) observed *Atlanticus* eating disabled individuals of *Melanoplus b. bilituratus,* and Davis (1893) found it fond of various fruits ranging from raspberries to watermelon. It is evident that *Atlanticus* should be classed as omnivorous-carnivorous, having a strong preference for animal foods obtained by predation and scavenging but often eating vegetable materials, especially fruits.

Many members of the Decticinae possess food-habits similar to those of *Atlanticus,* while some have a wider and some a more restricted range of diet. The Mormon cricket (*Anabrus*) and the coulee cricket (*Peranabrus*), outbreaks of which may do great damage in the western United States, have even greater latitude in their food selection than does *Atlanticus.* According to Corkins (1923), Gillette and Johnson (1905), La Rivers (1944), and

[13] A detailed analysis of the feeding behavior of this insect is now in preparation by the author. It includes a total of 39 feeding records not here listed.

Melander and Yothers (1917), these shield-backs feed indiscriminately on grains, native grasses and forbs, garden vegetables, dung, urine, and dead and dying animals of all kinds, often members of their own species. In fact, Swain (1940) discovered 403 species of plants on which *Anabrus* feeds, to say nothing of its carnivorous and cannibalistic propensities. However, *Peranabrus* was said by Snodgrass (1905) to be largely a scavenger on the dead and dying when in stationary bands and phytophagous when in migrating bands.

In contrast to the above highly omnivorous shield-backs, *Pediodectes* is almost restricted to an animal diet obtained largely by predation, though it feeds to a limited extent on the flowers and fruits of certain forbs (Isely, 1941). *Decticus,* which is known to feed voraciously on acridids, is even more restricted to an animal diet (Teyrovský, 1951). The species of *Aglaothorax, Idiostatus,* and certain other western genera were said to feed principally on leaves of dicotyledonous plants (Tinkham, 1944), though Rehn and Hebard (1920) found *A. segnis* only on *Juniperus.* Another species, *Acrodectes philopagus,* feeds on lichens (Rehn and Hebard, 1920; Tinkham, 1944), the only vegetable materials available in its barren, rocky alpine habitation.

In summary, it is probable that many species of the Decticinae, like *Atlanticus testaceus,* are omnivorous-carnivorous, but this behavior may be by necessity rather than by preference. When their preferred animal foods, which are taken by predation and by scavenging, are not available, they eat fruits, flowers, and foliage of living plants. Some species depart from the above diet, being primarily predators, while others are largely vegetarians.

Gryllidae, Gryllinae and Nemobiinae: Field and Ground Crickets

The Gryllinae and Nemobiinae, insects of incompletely nocturnal, largely geophilous habits, are sufficiently close in morphology and in feeding behavior to be discussed together, and in the past there has been some question whether they should be combined into a single subfamily. The mouthparts of the gryllines and nemobiines examined in this study proved to be of

omnivorous type, but they tend toward the forbivorous. Analyses of the insects' crop contents and fecal materials showed an extremely varied diet, the components of which were: in greatest amount, organic debris and dicot leaf materials; in lesser amount, insect remains; and, in least amount, spores, pollen, fragments of grass leaves, and sand grains. Caged individuals of *Acheta pennsylvanicus* ate, in approximate order of decreasing preference, meat, oat flakes, lettuce, and bran flakes, all of which were readily accepted. *A. domesticus* was also maintained in the laboratory, with approximately the same results. Several feeding records were obtained in nature: *Acheta pennsylvanicus* was twice seen feeding on animal remains and once each on mucous, oak flowers, and grass spikelets; and *Nemobius* was found nibbling on inflorescences of *Daucus*. Numerous individuals of *Acheta* and *Nemobius* were seen feeding on oatmeal trails (Gangwere, 1958).

The literature on feeding in Gryllinae is very extensive. In consequence, a somewhat limited number of salient references is given below.

Savin (1927) discovered that *Acheta* accepts as food any of forty-two different kinds of materials, including fats, proteins, and minerals, as well as rubber, which proved to be an especial delicacy. Severin (1926) and others inferred, however, that it is normally somewhat more restricted, being a vegetarian which selects widely from among many different plants in its habitat, preferring flowers and fruits but eating all parts of its foodplants, both living and dead. Obviously a scavenger, it is reported to relish fresh cow manure (Wolcott, 1923). It has been reported taking animal foods, particularly insects, by scavenging. Among the latter records are ones of feeding on dead birds, mammals, reptiles, and amphibians (Severin, 1926); dead insects, especially grasshoppers (Putnam, 1947); and crickets, moths, cockroaches, and tiger beetles (Folsom, 1931; Folsom and Woke, 1939). *Acheta* is also known to prey on eggs of *Mantis religiosa* (James, 1945) and on those of grasshoppers (Criddle, 1925). Only McColloch (1915), who watched a cricket devour eleven termites emerging from their holes, has noted aggressive predation in this genus.

The economic literature is replete with accounts of damage by *Acheta* to various crops, including grains, corn, tomato, cotton, clover, sweet potato, pea, bean, tobacco, mushrooms, strawberry, cranberry, canteloupe, watermelon, squash, pumpkin, beet, and carrot. The insect generally eats the foliage of these plants, but sometimes it eats the flowers, fruits, stems, and even roots. Similar records are listed for the less-destructive genera *Anurogryllus* (Caudell, 1904), *Gryllodes* (Caudell, 1908), and *Nemobius* (Blatchley, 1920).

It would appear, on the basis of the present study, that *Nemobius* has food-habits similar to those of *Acheta*. Information supplied by Richards (1952) supports this conclusion. He studied *Nemobius sylvestris*, a European species, in the laboratory and also obtained feeding records in nature, once on pomes of apple, and several times on various fungi. He concluded that the cricket's diet is largely composed of fungi, including molds and mildew, but that dead insects, fallen acorns, leaf galls, and honeysuckle foliage are supplementary items of food. He further asserted that animals are eaten by *N. sylvestris* only when dead or very weak. A relative, *N. allardi*, is also known to scavenge animal materials; Cantrall (1943) discovered the latter eating a dead *Peromyscus*. Caged individuals of both *Nemobius* and *Acheta* were frequently observed in the present study feeding on injured and weakened individuals of their own and other species, which is an act intermediate between predation and scavenging. *Nemobius*, like *Acheta*, eats eggs of *Mantis religiosa* (James, 1945).

While there are few detectable differences in the food-habits of the above-described native species of *Nemobius* and *Acheta*, a member of the latter genus, *A. domesticus*, differs notably. This species, which was reared in the present investigation, is a house-dweller having food-habits similar to those of domestic cockroaches. It eats dead insects, cloth, paper, bread, sugar, bran and oat flakes, fruits, meat, and other foodstuffs.

In summary, ground and field crickets are incompletely nocturnal and omnivorous or perhaps omnivorous-herbivorous, eating many different kinds of foods but showing great preference for plant materials, especially flowers and fruits. They are not

usually predacious or, at least, aggressively so, but they feed avidly on the dead bodies of all animals, which, in their habitations, are usually insects. They probably are not cannibalistic in nature, except on weakened or newly dead individuals of their species. One cricket, *Acheta domesticus,* has food-habits like those of domestic cockroaches.

Gryllidae, Oecanthinae: White Tree Crickets

The mouthparts of the Oecanthinae, like those of the other crickets here studied, are of modified omnivorous type, though their diet is somewhat more specialized. In the field these nocturnally active animals were often seen eating forb flowers and sometimes forb leaves, prey, and leaves of woody plants. In the differential feeding tests the tree crickets selected only forb flowers, but when lettuce was provided alone it was greedily eaten, for in succulence and texture it is apparently very similar to floral materials. Animal food was not provided but doubtlessly would have been taken. Insect remains and organic debris predominated in the crop contents and fecula; and spores, dicot pollen, and dicot leaves were common. These observations accord well with those of Fulton (1926), who found that oecanthines eat fruits, leaves, floral parts, and fungus fruiting bodies, as well as small, easily captured insects.

While the total amount of plant materials eaten by oecanthines probably surpasses that of animal materials, the latter may be preferred when available, or so one would suppose on the basis of their fiercely aggressive manner during predation. They were observed rapaciously eating aphids during the present investigation. This type of behavior was noted previously by Houghton (1904, 1909), by Knowlton (1947), and by other entomologists. According to Parrott and Fulton (1914), the white tree crickets feed on scale insects, small bugs, leafhoppers, various small wasps, and other soft-bodied insects. Murtfeldt (1889) reported that her crickets perished without animal foods, but whether their presence is imperative is uncertain. Fulton (1915) found that cannibalism is not infrequent, for nymphs which are unable to free themselves from their egg shells are

eaten by their fellows. Some students of the group have concluded that adults may be more phytophagous than are immatures and, hence, that predation diminishes with increased maturity (Comstock, 1881; Parrott and Fulton, 1914; Riley, 1889), but there is no recent information on this point.

In summary, the Oecanthinae, insects of nocturnal habit, feed on a limited assortment of foods compared with other kinds of Michigan crickets, restricting themselves principally to flowers and prey but also taking certain forb leaves and fruits. Aphids are among the most common prey eaten by these delicate but voracious insects, but they also eat many other small, soft-bodied insects.

Gryllotalpidae: Mole Crickets

Only one species of mole cricket, *Gryllotalpa hexadactyla,* was studied. The crop contents of several of these burrowing insects were largely composed of insect remains and organic debris, but they also included particles of dicot leaves. The mouthparts, as one would suspect from the above analyses, were of modified omnivorous type. One individual was caged. For a short time before dying, it ate roots of grasses.

The Gryllotalpidae are fossorial forms *par excellence.* As has often been noted in the literature, they use their modified fore legs much as do moles to burrow through loose soil. Authors differ about the relative amount of plant and animal foods consumed by these omnivores. Weiss and Dickerson (1918) discussed this point. Mole crickets are said to eat the tender roots of plants, either living or dead, and also fruits and foliage on the surface of the ground (More, 1924; Chittenden, 1903). Though Barrett (1902) and Van Zwaluwenburg (1918) reported that a relative of *Gryllotalpa, viz., Scapteriscus,* feeds almost wholly on living plants, other authors have emphasized the carnivorous habits of mole crickets. Thus, Craighead (1950) found that they feed on insects and earthworms, as well as on roots, and Chopard (1938) described them as voracious predators on worms, snails, and crickets. Baumgartner (1911) discussed their cannibalistic habits and Thomas (1928) their strong attraction for fresh horse droppings.

In summary, the Gryllotalpidae are fossorial insects of omnivorous food-habits, eating, among other things, roots of plants, either living or dead, and bodies of animals, including insects and earthworms.

REVIEW OF FOODS TAKEN BY ORTHOPTERA

In light of the foregoing account of feeding in the groups and species of Orthoptera it is apparent that the food-habits of these insects are extremely varied. So diverse are they that it is perhaps necessary to reconsider and clarify them, this time on the basis of food categories. This need is answered in the following section. Citation of feeding records will not be included below, except where records have not been given in the preceding section.

The diet of Orthoptera consists of numerous kinds of food substances, including both plant and animal materials. The former are taken in the form of (1) *plant products and secretions,* (2) *dead plant materials,* and (3) *living plants,* both wild and cultivated.

Numbered among the *plant products and secretions* in the diets of Orthoptera are foodstuffs, *e.g.,* flakes of bran and oats and bread, which are eaten by *Acheta domesticus* and domestic cockroaches; cloth, eaten by *A. domesticus* (Kemper, 1937), *A. pennsylvanicus,* certain Acrididae (field notes of author), *Ceuthophilus,* domestic cockroaches, and *Gryllodes* (Davis, 1914); rubber, eaten by *A. pennsylvanicus;* paper and cardboard, eaten by *A. domesticus,* domestic cockroaches, and the stick-insect *Carausius* (Sargent, 1937); paste, eaten by *A. domesticus* and domestic cockroaches; and extrafloral secretions, eaten by *Ceuthophilus, Conocephalus* (Nishida, 1958), and others.

The *dead plant materials* eaten by Orthoptera include both newly dead and well-decomposed substances. While the consumption of both are examples of saprophagy, the former is close to phytophagy. Such materials compose considerable parts of the diet of the Blattidae, Gryllinae, Gryllotalpidae, Nemobiinae, Rhaphidophorinae, and Tetrigidae.

Of considerable interest is the fact that many Orthoptera accept dead, dry vegetable materials of a type they would not

ordinarily accept in the living, green condition. Examples are *Chloealtis,* a graminivore, eating dried, brown leaves of *Fragaria* (wild strawberry); *Scudderia c. curvicauda,* a forbivore, those of the sedge *Carex tribuloides;* and *Arphia sulphurea,* a graminivore, those of *Quercus velutina* (oak).[14] Certain graminivorous acridines (Anderson and Wright, 1952) and *Melanoplus b. bilituratus* (Scharff, 1954) ate dead, dried plant materials found on the ground. These records suggest that much of the specificity which grasshoppers and their allies exhibit in selection of living food-plants may be lost on death and desiccation of the plants.

The *living plants* eaten by Orthoptera include a wide assortment of both juvenile and mature forbs, grasses, sedges, rushes, horsetails, ferns, mosses, algae, fungi, and lichens, as well as woody plants, including both evergreen and deciduous trees, vines, and shrubs.

Belocephalus sabalis, certain Cyrtacanthacridinae, *Microcentrum rhombifolium* and certain other Phaneropterinae, and most Phasmidae, which select as food the leaves of deciduous trees or shrubs, both sapling and mature, are among the Orthoptera which eat woody plants. *Morsea californica* (Ball, 1936), *Melanoplus punctulatus,* and *M. splendidus* eat the foliage of coniferous trees. The first of these, *Morsea,* also has been recorded perched on *Arctostaphylos* (Rehn and Hebard, 1909a). While the stems and roots of woody plants are not usually attacked by grasshoppers and allies, the decaying wood of chestnut, fir, and pine offers both shelter and sustenance to the gallery-making cockroach *Cryptocercus,* the symbiotic intestinal fauna of which enables it to digest its cellulose-laden food.

All parts of forbs or broad-leaved herbs, especially their leaves, are accepted by one or another of the Orthoptera. In fact, most members of every Michigan group except the Acridinae, Copiphorinae, Mantidae, and Phasmidae take, in one form or another, such materials. The Blattidae, Conocephalinae, Cyrtacanthacridinae, Decticinae, Dermaptera, Gryllinae, Nemobiinae, Oecanthinae, Oedipodinae, Phaneropterinae, and Tetrigidae regularly

[14] This *Arphia* record, one not contained in the present report, will appear in a paper now in preparation.

or occasionally eat forb leaves and, usually to a lesser extent, their stems and reproductive parts. In addition, the Blattidae, Gryllinae, and especially the Gryllotalpidae frequently eat forb roots and stems, and the Blattidae, Decticinae, Dermaptera, and Oecanthinae reproductive parts of forbs, including their flowers and fruits.

Grasses, sedges, and rushes are here grouped as a single food-type because of their essential similarity in form, texture, and silica content and because of their similarity in terms of attractiveness to Orthoptera. The leaves and, to a lesser extent, the stems and reproductive parts of these monocots are eaten regularly by the Acridinae, Cyrtacanthacridinae, and Oedipodinae, the first of these three groups largely being restricted to them. The Tetrigidae sometimes eat sprouts of grasses. Furthermore, certain Dermaptera feed on grass pollen, and the Conocephalinae and Copiphorinae eat the flowers and fruits of these plants. The Gryllotalpidae eat their roots.

Other types of living plants, including horsetails and scouring rushes, ferns, mosses, algae, fungi, and lichens, are much less commonly accepted as food by Orthoptera but are, notwithstanding, sometimes taken in quantity by certain species. Horsetails and scouring rushes of the genus *Equisetum* are quite acceptable as food to numerous caged Oedipodinae and Cyrtacanthacridinae, and they must be a commonly selected food of these insects in nature. Ferns, however, are seldom food for Orthoptera, though the phaneropterine *Scudderia septentrionalis* may sometimes eat *Pteridium,* and certain species of *Ceuthophilus* proved to have fern spores among their crop contents. The cricket *Hapithus* is recorded as having fed especially on ferns in greenhouses (Morse, 1916, 1920).

Various scavengers, including certain Dermaptera and many Blattidae, Gryllinae, Gryllotalpidae, Nemobiinae, and Rhaphidophorinae are either suspected or known to select as food the lower plants. Mosses are a particular favorite of the Tetrigidae, which are also known to eat algae, fungi, and lichens. Grasshoppers may feed on lower plants, for certain Cyrtacanthacridinae and bare-ground Oedipodinae were here found to have such habits. The Oecanthinae, which normally eat flowers and leaves

of higher plants and bodies of small insects, are known to eat fruiting bodies of fungi. The decticine *Acrodectes* has been reported a lichen-feeder, and indeed there is no other food available in its alpine habitat. The earwig *Forficula* is known to eat mosses, lichens, algae, fungi, and probably ferns.

In general, plant materials are more frequently taken by Orthoptera than are animal ones, but this does not mean that the latter diet is uncommon. Carnivorous food-habits are well developed in many groups, sometimes to the complete exclusion of phytophagy. Animal foods may be selected in the form of (1) *animal products, wastes, or secretions;* (2) *dead animal materials;* and (3) *living animals.*

The *animal products, wastes, or secretions* eaten by Orthoptera include dung and excrement, which are taken by many Acrididae, Blattidae, Decticinae, Gryllinae, Gryllotalpidae, Nemobiinae, Rhaphidophorinae; mucous, taken by certain Blattidae and Gryllidae; perspiration, taken by Blattidae and Gryllidae, as well as by certain Conocephalinae,[15] Cyrtacanthacridinae,[15] and Oedipodinae;[15] toenails and hair, eaten by cockroaches (Gates, 1912; Lugger, 1898); epidermal secretions, eaten by *Myrmecophila* (Wheeler, 1900; Beall, 1929); glue and leather, eaten by *Acheta domesticus* and domestic cockroaches; and, finally, household meat or meat products, eaten by *A. domesticus* and domestic cockroaches.

There are two distinct classes of food which may be considered under the heading of *dead animal materials.* These classes include old, partly decomposed materials and fresh, newly dead ones. The former are eaten by a host of Orthoptera, including members of the Blattidae, Conocephalinae, Decticinae, Dermaptera, Gryllinae, Gryllotalpidae, Nemobiinae, and Rhaphidophorinae. The latter, newly dead materials, which are really somewhat intermediate between dead and living substances, are taken by all of the above insects, as well as by the Cyrtacanthacridinae and Oedipodinae and perhaps rarely by certain Phaneropterinae.

The last class of animal food, *living animals,* composes the diet of a surprisingly large number of groups of Orthoptera.

[15] Field notes of author.

Some species eat normal, active prey which they catch by overtaking it, by stalking it, or by lying in wait for it to move close enough for capture. The more powerful, faster of them eat virtually anything which they can catch and overpower, including some large, heavily sclerotized insects. Among them are *Clonia* (Akerman, 1932), *Saga* (Bérenquier, 1905; Burr, Campbell, and Uvarov, 1923; Chopard, 1946), and *Rehnia*,[16] which are exotic katydids of the Saginae and Listroscelinae; certain Decticinae (*Decticus, Pediodectes*) and Rhaphidophorinae (*Tachycines, Udeopsylla*); and most of the Mantidae, which are so voracious and powerful that few insects are able to escape them, and which overcome even small vertebrates.

Other predacious but less powerful Orthoptera usually prey on smaller, weaker, more soft-bodied insects, ranging from aphids to nymphal grasshoppers but sometimes including larger, clumsy, slow-moving katydids, caterpillars, and other insects. Among these latter predators are the Conocephalinae; the Oecanthinae, which are fierce predators on aphids; the Gryllotalpidae, which are said to be predacious on insects and earthworms; and certain Blattidae (*Blatta orientalis,* said to be a bedbug predator); Dermaptera; and Gryllinae (*Acheta* eating termites).

An even larger number of Orthoptera take living animal materials in the form of teneral, injured, weakened, or dying prey. If the prey is close to death and not moving actively, it may be passed up by mantids and other more powerful predators, but most of the above predacious Orthoptera willingly accept weakened prey. Some additional groups not usually considered predacious also may accept such prey; the Blattidae, Cyrtacanthacridinae, Gryllinae, Oedipodinae, Rhaphidophorinae, and perhaps the Nemobiinae are numbered here.

In most cases the prey consists of species different from that of the predator, but virtually all of the above groups of predacious Orthoptera will occasionally prove cannibalistic, and the Mantidae, certain Decticinae, Listroscelinae, and Rhaphidophorinae, and, to a lesser extent, certain Conocephalinae practice cannibalism regularly.

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[16] Laboratory notes of author.

REVIEW OF FACTORS WHICH INFLUENCE FOOD SELECTION IN ORTHOPTERA

Earlier sections of this work featured discussions of (1) the techniques used in the study of food selection, (2) feeding in the groups and species of Orthoptera, and (3) the food categories selected by Orthoptera. These sections were based on data amassed during numerous field and laboratory studies. An evaluation of the reliability of these studies as a basis for conclusions on food selection seems appropriate. Such an evaluation requires an inquiry into the various factors which modify and determine food selection and the manner in which these agents operate.

Climate as a Factor in Food Selection

Climate, as well as microclimate, exert an influence on the feeding behavior of Orthoptera. Air and ground level heat, humidity, and wind act separately and together, both on the feeding insects and on the vegetation or animals on which they feed. The effects of these agents are modified by features of the topography and by density of the plant cover, which determine the degree to which the insects are sheltered.

Heat, Humidity, and Light.—Within the limits of their tolerance, insects, like other poikilotherms, become more active as the temperature rises. Up to a point, their feeding activities increase more or less in proportion to their body temperature (Gangwere, 1958), but, as shown in certain locusts (Hussein, 1937), restlessness and movement become so marked at the upper limits of their temperature tolerance that feeding diminishes or ceases. In an attempt to escape oppressive heat, individuals of *Nomadacris septemfasciata* regularly mount the vegetation and turn their bodies in order that the least possible surface is presented to the rays of the sun (Faure, 1935). Other locusts are known to do the same. Conversely, lowered temperatures cause lessened activities. Thus, many sun-loving grasshoppers become absolutely immobile during the night, and often they seek shelter under rocks and in cracks in the ground during cold weather. During the first cool autumn evening there is a marked decrease in the singing and other activities of nocturnal katydids and

crickets. According to Walker (1937), *Grylloblatta,* which normally dwells under conditions of extremely low temperatures, needs food only once in three or four months and consumes less in a year than do many species in a day.

Rain operates both in the increase of humidity and as a mechanical factor. Thus, the sheer pounding of rain drops on insects, usually accompanied by increased velocity of wind, makes difficult their movements. Furthermore, insects are organisms of small size and, therefore, of comparatively large surface area with respect to volume. As a consequence, their bodies have a marked affinity for water, sometimes with fatal results. It should not surprise one to discover that most Orthoptera, like those observed here, probably cease feeding and seek shelter under leaves and other objects in their haunts during rainstorms. *Ischnoptera,* studied by Rau (1947), may offer a partial exception, for that author found that cockroaches of this genus maintain their positions atop vegetation during a drizzling rain.

The locust *Chortoicetes* moves into open fields from surrounding woodlands because of its positive phototaxis (Clark, 1950). The mere passage of a cloud obscuring the sun causes *Arphia sulphurea* and certain other oedipodines to cease movement (Gangwere, 1959a). The effects of the change in light are perhaps reinforced by an accompanying drop in body temperature resulting from the reduction in radiant energy. Similarly, many nocturnal Orthoptera are extremely sensitive to changes in light intensity. *Atlanticus testaceus,* for example, crouches when a beam of low intensity light is directed on it, and *Ceuthophilus* has proved to be at least equally sensitive to light (Gangwere, unpublished).

Daily variations in heat, humidity, and light control the daily rhythm of Orthoptera, including their feeding periodicity. On the latter subject there is a rather extensive literature. Parker's study on the two grasshoppers *Melanoplus b. bilituratus* and *Camnula pellucida* (1930) demonstrated the important role of temperature and humidity in regulation of feeding activities. The present author's paper on periodicity of feeding (1958) assembled some literature pertinent to the subject and described the three general patterns of periodicity found in Orthoptera, *viz.,* the diurnal, nocturnal, and incompletely nocturnal patterns.

Wind.—To a degree, wind operates somewhat independently of the above climatic agents. Hubbell (1936) discovered that *Ceuthophilus* is very sensitive to wind currents. Records by Shotwell (1930), Hastings (1948), and certain field observations made during this study indicate that feeding and movements of Orthoptera are depressed by excessive wind. Nevertheless, the role of this factor in modifying the animals' behavior, though it cannot be discounted, is probably not a major one.

For a detailed analysis of insects and climate the reader is referred to Uvarov's discussion (1931).

Food as a Factor in Food Selection

The attractiveness, availability, and condition of possible foods are factors which must be taken into account in studying the food selection of Orthoptera.

Attractiveness.—The attractiveness of a food is determined by the response of the feeder to the physical and chemical characteristics of that food. Some of the physical characteristics of food-plants are the comparative presence or absence of spines, dense pubescence, hard cuticle, thick leaves, and tough, fibrous tissues, which may make the food difficult or easy to approach, to bite into, or to chew. The role that toughness of leaves plays in food selection of acridids, particularly young ones, was discussed by Williams (1954). Bredemann (1941) found a certain maize and a sweet-corn with dense pubescence resistant to locusts, and Van der Merwe and Kent (1925) found stiff, succulent leaves resistant to *Zonocerus*. To the contrary, in this study, the prickly leaves of *Cirsium* (thistle) proved highly attractive to various grasshoppers, and the coarse, siliceous leaves of *Equisetum* (horsetail), though not a favorite, were often eaten by grasshoppers.

Essential oils, resinous substances, milky saps, and other chemical substances may make plants attractive or repulsive. One or another of the plant genera *Azadirachta, Calotropis, Melia,* and *Scylla* were noted by Bhatia (1940), Chauvin and Mentzer (1951), Roonwal (1953), Sergent and Poncet (1951), and Volkonsky (1937) as containing repulsive substances which inhibit feeding by various locusts; leaves of *Eucalyptus, Citrus*

nobilis, Papaver, Oleander, and *Glycirrhiza* were found locust resistant by Bredemann (1941); and Williams (1954) suspected that the aromatic, resinous oils of the gymnosperm *Cupressus* act as a repellant to feeding by certain grasshoppers he studied. The latter may explain why, as noted in the present investigation, few Orthoptera eat gymnosperms.

In contrast, the grasshopper *Schistocerca ceratiola* feeds only on the odoriferous, highly resinous foliage of *Ceratiola ericoides* (Hubbell and Walker, 1928). Similar records are available for *Lea* (Hebard, 1941) and for a number of Orthoptera which feed on the sticky, pungent leaves of *Larrea* (Ball *et al,* 1942; Isely, 1944; Tinkham, 1944). Furthermore, various composites, milkweeds, and mints characterized by colored saps and special odors proved attractive to a wide assortment of grasshoppers, katydids, and crickets during the course of this study.

Succulence of foods is a factor in food selection. Flowers of forbs proved especially attractive to phaneropterines and various other Orthoptera in this study; lettuce, a food equal in succulence to flowers, proved to be almost a universal food; its relative *Lactuca* (wild lettuce) is especially attractive to many grasshoppers; and, in general, green, succulent vegetation is preferred by leaf-feeders to dried, brown leaves, though some exceptions are noted on pp. 113, 114. Nevertheless, water content does not always appear to be of major significance, for Roonwal's study of *Schistocerca* (1953) and Vuillaume's on *Zonocerus* (1953) showed no apparent correlation between preference value and water content.

Much of the difference in attractiveness of the food-plants tested in the present investigation probably depends on odor and taste, but the choice made between grasses and forbs is primarily a matter of the structure and texture of the leaves.

Carnivorous Orthoptera appear to be much less selective than are phytophagous species. As discussed in a preceding section of this report, mantids show practically no preferences, except those based on size of prey. It is possible, however, that a few butterflies and ants are repulsive and certain beetles so effectively armored that they may be immune to attack by mantids. In general, orthopteran carnivores eat the soft, succulent parts and leave untouched the wings, tarsi, and certain other hard

parts. One must conclude, therefore, that palatability, mechanical characteristics, and succulence of food are factors in the selection of both plant and animal materials.

Availability.—The degree to which a given type of food is subjected to feeding is as much determined by its availability as by its attractiveness. An acceptable species, either plant or animal, may be present or absent, abundant or scarce, generally distributed or localized with respect to a given community. Thus, a plant absent from a community cannot be eaten there, though its preference value may be high. Furthermore, abundant plants are more likely to be eaten than are scarce ones, and plants uniformly distributed in a community are more likely to be fed upon, at least by generally distributed feeders, than are those localized in patches, though the plants may be present in equal numbers. This latter is explained by the fact that Orthoptera tend to eat the first acceptable food they encounter, instead of seeking more highly preferred ones. From this point-of-view, therefore, their choice of food may be said to be based in large part on chance encounter and availability.

Availability changes with the season, as various plants grow, mature, and die, and others take their places, and as particular plant parts, *e.g.*, flowers and fruits, appear and disappear. Among the Cyrtacanthacridinae, for example, there is a shift from grass-feeding in the spring to forb-feeding in late summer as annuals of this latter group become proportionately more available. Pfadt (1949a) observed a seasonal shift of food-plant in *Aulocara elliotti*. *Acrolophitus variegatus* and *Melanoplus texanus* may also be species whose periodism is linked with that of their food-plants (Isely, 1937).

Most species of Orthoptera were shown by the present feeding experiments to have food preferences which can seldom, if ever, be satisfied in nature because these foods are not present in the normal habitations of the feeders. Thus, countless species are fond of lettuce, a food they never encounter in nature. Similarly, the arid-land *Aeoloplides chenopodii,* whose normal food is saltbush and greasewood, is at certain times a pest on apple trees grown under irrigation (Wallace, 1955); caged *Hadrotettix trifasciatus* was reported by Isely (1938) to have fed entirely

on two species of *Euphorbia* which do not occur in its habitat; two grasshoppers, *Melanoplus bivittatus* and *M. d. differentialis,* were found highly attracted to a citrus and a palm, neither of which grow in their normal habitation (Mail, 1931). Preferences for given plants, no matter how great they may be, are meaningless in their absence.

Carnivorous Orthoptera, as noted previously, are generally much less selective than are phytophagous species. Their diet tends, therefore, to be determined largely by food availability, which, in turn, depends on their habitat selection, on the periodism or seasonal availability of their prey, and on possible competition for their prey.

Size and Condition of Food.—The feeding of phytophagous species is regulated in part by differences in the physiological and developmental condition of their food-plants. Wilting and progressive seasonal desiccation reduce the acceptability of various plants to Michigan Orthoptera. Thus, *Agropyron*, a favorite of many acridids in spring and early summer, and *Bromus inermis,* the grains of which are eaten avidly by *Neoconocephalus* early in the season, are largely ignored in the fall as they become dry and brown. *Schistocerca obscura* undergoes a similar seasonal change in its food selection (Duck, 1944). In India, according to Husain, Mathur, and Roonwal (1946), *Capparis aphylla* is an important food of *Schistocerca gregaria* during middle summer but is unpalatable to this insect during late winter and early summer.

Developmental changes in plants influence feeding. As plants grow, they become increasingly inaccessible to ground-dwelling Orthoptera, and as their tissues become tougher and more fibrous they may become less attractive. Development of new parts accompanies growth and maturation of the food-plants. These parts may also be eaten but often are either more attractive or less attractive than are earlier parts. This latter agrees with Roonwal's conclusion (1953), *viz.*, if one part of a plant is acceptable, all parts are usually acceptable, but differentially so. It is not surprising, therefore, to find that there is an unusually high incidence of feeding by many species on the flowers of

plants newly in bloom. Thus, *Conocephalus f. fasciatus,* a species seldom observed feeding in nature during this study, was once seen in large numbers eating the new flowers of *Agrostis.*

In the case of animal foods or prey, there are also physiological changes which modify the likelihood of feeding. The weakening of potential prey by oviposition, disease, hunger, etc., makes them more readily overpowered and eaten. This may explain in part the increased cannibalism noted among starved, caged orthopterans.

Size of prey is important. Small insects, including aphids and *Drosophila;* medium-sized ones, such as houseflies; and large ones, including blowflies and adult grasshoppers, are appropriate foods for, respectively, early instar, middle instar, and adult mantids (Didlake, 1926). This progression of size in food selection of predators would appear to be a general rule. Most attack the largest prey which they can overpower, and frequently they ignore smaller prey. The powerful *Saga,* as pointed out earlier, overcomes and eats the large carnivorous katydid *Tettigonia,* and mantids even eat small mammals and birds. In contrast, the voracious but much smaller *Oecanthus* eats mostly small, weak, soft-bodied aphids.

The Feeder as a Factor in Food Selection

Feeding behavior is markedly affected by the condition of the feeder, as determined by physiological, developmental, and other factors.

Hunger and Thirst.—The degree of hunger of a feeder is dependent on the length of time since its last meal, the amount eaten at that time, the rapidity with which digestion and elimination proceed, and the cumulative effect of recent meals. Selective responses to different foods diminish as hunger increases. Thus, starvation may alter normal feeding habits. The author's studies disclosed that *Chortophaga,* which is predominately a grass-feeder, will, when hungry, eat virtually any fresh forb which is offered; under pressure of starvation some strictly graminivorous acridines will eat sparingly of certain forbs, though they usually cannot survive on such a diet; certain acridids, normally phytophagous, become somewhat cannibalistic

under starvation pressure; and, under these conditions, certain mildly predacious crickets develop marked cannibalism. Nevertheless, many species starve rather than eat foods different from those which they normally select in nature.

On the basis of earlier work (Gangwere, 1960b), it is believed that most Orthoptera usually do not drink in nature but obtain unbound water from their fresh, non-dry foods. Hence, a part of their changed response during starvation is probably the result of thirst. This contention is supported by statements by Bodine (1921), who found that grasshoppers, when starved, rapidly lose weight because of a reduction in the percentage of water in their body, and by Beier (1934), who noted that death from starvation is more delayed under conditions of high relative humidity than under those of low relative humidity. It follows that, when the weather is hot and dry and their foods become desiccated, many species become quite voracious and are attracted to anything moist, including earth, dampened cloth, and succulent foliage. *Acheta* (Criddle, 1925), various acridids (Williams, 1954; Shotwell, 1941), and *Chortoicetes* (Clark, 1947) will serve as examples.

Injury, Disease, and Parasitism.—Injury, disease, and parasitism presumably have their effect on the activities of Orthoptera, including their feeding, but the extent to which these factors operate and the manner in which they do so is not easy to demonstrate, except where the injury is severe or the disease or parasitism far advanced. The most common injury, loss of a leg, which is so frequent among the saltatorial forms, has no apparent effect on their feeding behavior and does not even seriously interfere with their motility.

Orthoptera are hosts of a considerable number of bacteria, protozoans, and entomogenous fungi, some of which are pathogenic to them. Observations on diseased and parasitized individuals are beyond the scope of the present study, but the work of others demonstrates that infection by some parasites has a pronounced effect on feeding. Numerous papers describing one or more aspects of parasitism and disease in various Orthoptera are available, and detailed discussions in cockroaches and in acridids were given by, respectively, Roth and Willis (1957)

and Uvarov (1928). However, the material given below, except where indicated, is taken from Sweetman (1936) and Steinhaus (1946, 1952).

Many grasshoppers and some crickets are susceptible to certain strains of the bacterium *Coccobacillus acridiorum,* which sometimes causes epidemics in outbreak populations of the species of *Schistocerca.* Cannibalism under crowded conditions is believed to be partly responsible for creation of such epidemics. Susceptibility varies among different species of grasshoppers, and the virulence of different strains of the pathogen also varies and can be increased by passage. As the disease progresses, the host displays lessened and failing appetite and decreased activity, accompanied by rectal and oral discharge.

The most common of the fungi causing disease in Orthoptera is *Empusa grylli,* which attacks a wide range of species and sometimes causes epidemics among grasshoppers, especially under conditions of high density of population, high temperature, and high humidity. Often the first symptoms are lessened response to stimuli and reduced movement; later the insects may lose ability to maintain their equilibrium.

Among animal parasites, the gut-inhabiting Protozoa of the sporozoan group Gregarinida are especially characteristic of Orthoptera. Heavy infestations may produce debilitating disease, though they seldom cause death. Many roundworms parasitize Orthoptera. Some, like the nematode *Cephalobium microbivorum,* found in *Acheta,* live in the digestive tract, but others, such as the "hair-snakes" *Gordius* and *Paragordius* and the mermithids *Mermis* and *Agamermis,* occupy the body cavity or tissues of the host. The most common roundworm parasite of grasshoppers in the eastern United States is *Mermis subnigrescens.* During the present study, individuals of *Melanoplus k. luridus, M. bivittatus, M. s. scudderi, Orphulella speciosa,* and *Pseudopomala brachyptera* were found to be parasitized by mermithids, probably of the latter species. The larvae of various larvaevorid flies are also frequent parasites in grasshoppers and less often in katydids, camel crickets, and crickets.

The literature gives no obvious differences in feeding behavior of Orthoptera parasitized by roundworms or fly larvae in the

earlier stages of development of the parasites, but, as the latter increase in size to the point of filling much of the body cavity, all of the functions of the host are deranged, and death accompanies or soon follows emergence of the parasites from its body.

Changes during Development.—Physiological changes accompanying growth, ecdysis, maturation of the gonads, the activities of courtship and mating, and old age have their effects on feeding.

Newly hatched young are generally unable to feed for a day or even longer after emergence, as has been shown in certain grasshoppers (Criddle, 1922; Valova, 1924; Van der Merwe and Kent, 1925), phasmids (Roth, 1917), and mantids (Gurney, 1951). In *Phyllium* (Leigh, 1909), there is a foodless period after hatching. It lasts for four days because it takes that long for the first-instar nymphs to climb from the ground, where the eggs are dropped, to the foliage of their food-plants. *Scapteriscus* may offer an exception to the above, for Hayslip (1943) and Van Zwaluwenburg (1918) reported that immatures of this mole cricket fight for food and begin feeding almost immediately after hatching.

It is generally accepted that Orthoptera do not feed immediately before, during, and after hatching. Muscle attachments are being shifted to the new exoskeleton; sclerites are hardening sufficiently to resist the pull of the muscles; and the mouthparts are not strong enough to be used in biting and chewing. Documentation of this point would appear unnecessary.

The feeding behavior of adult Orthoptera prior to the maturation of their testes and ovaries does not differ significantly from that of last-stage nymphs, but, with attainment of sexual maturity, the males, in particular, spend more time in sexual activity and less in feeding. While *in coitu,* males rarely, if ever, feed, and Ball (1915) noted that males of the grasshopper *Camnula pellucida* feed but little during the entire breeding period. The difference is less marked in the instance of females; many female grasshoppers and katydids of Michigan were found feeding considerably during copulation. However, this latter is partly offset by the fact that, at least in certain species, oviposition may inhibit feeding (Richards and Waloff, 1954) and may weaken them seriously (Melander and Yothers, 1917).

Advanced senescence of Orthoptera may be characterized by a gradual decrease in feeding until it ceases entirely, generally a few days before death. Rau and Rau (1913) reported that *Stagmomantis* consumes less and less food as old age is reached, and Roth (1917) found that *Carausius* may cease feeding for days at a time during old age.

Many of the changes in feeding behavior noted above, except for the last, are somewhat temporary in nature. Others, which are related to the insects' developmental polymorphism and their sexual dimorphism, are either longer in duration or progressive in nature. There is evidence to indicate the existence of a direct positive correlation between life stage and food consumption. Roth (1917) found that nymphs of the walking-stick *Carausius* double their food consumption in each successive stadium, and Langford (1930) noted that grasshopper nymphs almost double their consumption with each molt. The initial size difference between the first-stage nymphs of either sex is negligible, but it increases rapidly during growth, with a concomitant difference in the amount of food consumed. Females of the grasshopper *Melanoplus s. scudderi* consume more than do males, though they eat less per unit of weight (Gangwere, 1959). Females of certain grasshoppers eat 2.5 times more food than do males in a 12-hour period (Langford, 1930). Males of *Dichromorpha* are both shorter-lived and lighter eaters than are females (Rau, 1915), which is perhaps true for most Orthoptera. Males of certain grasshoppers feed for comparatively longer intervals of time, but females of these species feed more frequently (Williams, 1954).

Choice of food, as well as food consumption, may vary somewhat during the course of development. Among the strongly predacious mantids, as noted above, size and type of prey is roughly proportional to growth of the predator. Juvenile tree crickets (*Oecanthus*) are said to feed chiefly on aphids, while the adults are more herbivorous (Comstock, 1881; Parrott and Fulton, 1914; Riley, 1889). The opposite is true of *Forficula*, the immatures of which are more herbivorous than are adults (Crumb, Eide, and Bonn, 1941). The first-stage nymphs of the Moroccan locust in Transcaucasia feed almost exclusively on *Poa*

bulbosa, but with each molt the number of food-plants increases (Sviridenko, 1924). *Zonocerus,* a polyphagous pyrgomorphine, exhibits distinct preferences which become somewhat less pronounced from stage to stage during nymphal development (Vuillaume, 1953). Early-stage juveniles of the walking-stick *Diapheromera femorata* eat basswood leaves but do not touch those of oak, which are preferred by late-stage nymphs and by adults (Graham, 1937). Furthermore, the early instars of most phytophagous grasshoppers and katydids of Michigan probably select leaves of more delicate texture than do adults.

In view of the above, it cannot be questioned that food selection and food consumption may vary somewhat during the life stages and between the sexes of certain species, though such disparities are not marked. Notwithstanding the above, the results of the present study show no really significant differences between the food-habits of nymphs, especially half-grown and larger ones, and those of adult males and females, aside from differences in consumption related to differences in body size. Information from a number of investigators, including Barnes (1955), Beall (1932), Chopard (1938), Didlake (1926), Faure (1935), and Williams (1954) supports the above view of essential uniformity of food selection throughout the life stages and between the sexes of Orthoptera. Such other differences as may exist in the feeding of a given species are the result of (1) changes in the seasonal aspect of the vegetation, which coincide with different stages in the life history, and of (2) changes in behavior consequent on the attainment of sexual maturity and, in most species, the acquisition of flight.

Other Factors Affecting the Feeders.—Habit patterns, conditioned acceptance of certain foods, and degree of crowding may modify food selection.

Habit patterns which affect feeding may take the form of habitat selection, migration, or mating. Each may operate to extend or to reduce the variety of possible food choices among the food-plants or prey available to the feeders. Some acridids occupy many different situations in several communities and in each of them have available a somewhat different assortment of food-plants; *Melanoplus f.-r. femur-rubrum* is such a species.

Other more localized species have a comparatively reduced assortment of food-plants or prey from which to select. Geophilous Orthoptera, for example, are restricted largely to foods growing close to the surface of the ground, ones which arboreal species seldom encounter; the food selection of the geophilous mantid *Litaneutria* is necessarily different from that of other mantids, which are phytophilous. In contrast, the phasmid *Diapheromera femorata* moves into the tops of trees because of a response to a strong negative geotaxis and, hence, is separated from a preferred food, the shrub *Rubus*. *Atlanticus testaceus*, an incompletely nocturnal shield-back geophilous during the day, undergoes a nocturnal ascent of the vegetation; its food selection during the night, the period when it does most of its feeding, is, therefore, basically that of a phytophilous species. Slender, laterally compressed acridids select growths of tall grasses and sedges for habitation and feeding and seldom come into contact with the short, procumbent grasses which occur in more open situations; more dorsoventrally depressed acridids live in areas of short, procumbent grasses and forbs and feed accordingly.

Williams (1954) investigated certain aspects of habitat selection. He found that grasshoppers are attracted to a number of visual patterns including vertical stripes, which probably explains why upright blades of grass are preferred to those lying flat; and that leaves in a vertical plane are easier to chew than those which are horizontal, which might explain part of the insects' preference for grasses over forbs.

Nymphs of *Romalea* migrate from their hatching sites to low, swampy land where there is more succulent vegetation on which to feed (Watson, 1941). Migration is more pronounced in certain highly noxious species. *Anabrus simplex, Camnula pellucida, Chortoicetes terminifera, Locusta migratoria, Melanoplus spretus, M. b. bilituratus, Nomadacris septemfasciata,* and *Schistocerca gregaria* are merely a few of the many Orthoptera which migrate in bands, both as immatures and as adults. In so doing, these wide-ranging insects encounter a much greater variety of food-plants than do many of their more restricted relatives.

Mating habits following sexual maturity may sometimes lead to a change in habitat. This latter is preeminently true of the

plague locusts of the Old World, and in this country *Dissosteira longipennis* leaves its customary feeding grounds and migrates to breeding grounds where oviposition occurs (Corkins, 1923). Grouse locusts form seasonal mating aggregations (Cantrall, 1943), which habit may alter their available food assortment.

Mating may have other consequences. Copulation in mantids, as noted previously, is often accompanied by cannibalism, as the smaller male is eaten by the larger, stronger female. This seldom occurs at other times, when the males avoid the females. The same result was noted during copulation of *Ceuthophilus* (Turner, 1915) and *Grylloblatta* (Walker, 1937). It must also occur among certain of the voracious, carnivorous katydids.

The importance of conditioning in establishing particular food preferences has been noted in certain Lepidoptera and in other insects, but little is known of the extent to which it may operate in Orthoptera. Pfadt (1949) found that dandelion is a preferred food of *Melanoplus b. bilituratus* but detected no difference in the degree to which it is preferred among individuals captured in four different communities characterized by differences in vegetation. He concluded that conditioning does not exist in this species. In the present series of experiments, also, no evidence of conditioning was discovered, but tests were not devised to prove or to disprove its operation in the Michigan fauna. Sladden and Hewer (1938), however, reported an apparent transfer of induced food-habits from parent to young in the phasmid *Carausius*. Newly hatched nymphs descended from parents forced to eat ivy ate this plant more readily than did nymphs descended from parents fed on privet.

There is reason to believe that crowding in cages has a disturbing psychological effect on Orthoptera. Perhaps this explains, in part, the increased cannibalism that occurs among caged Orthoptera, particularly Tettigoniidae, even in the presence of ample food. It appears more likely, however, that the increased opportunities for cannibalism afforded by confinement and proximity of individuals account for this behavior. Crowding occurs under natural conditions in those species which occasionally or regularly increase to outbreak numbers, and under such conditions many of them commonly engage in cannibalism. The Mormon and Coulee crickets, various Old World plague locusts, *Tettigonia viridissima*, and the Rocky Mountain locust are

some of the Orthoptera which have been recorded as eating others of their kind which were injured, diseased, or incapacitated by molting or oviposition. How much of the above should be attributed to starvation pressure and how much to the psychological effect of crowding is uncertain.

It is apparent from the foregoing that various factors regulate or, at least, influence food selection in Orthoptera. Variations in these factors are responsible for many minor discrepancies in the present data and in those recorded in the literature. Much of the uncertainty, however, has been cancelled out in the present investigation by the experimental design used. In planning the experiments and in evaluating their results, efforts were made to eliminate the influence of as many variables as possible and to make allowance for those which could not be controlled. Field observations were carried out over a long period, and careful records were kept of the conditions under which they were made. Feeding experiments were, as far as possible, repeated many times and under known conditions.

Thus, food selection was studied by the observation of individuals feeding in the field, by analyses of crop contents and fecal materials, and by differential feeding tests. The first two measure the choice of food made by the insects in their natural environments as a result of their food preferences, the availability of their foods, and other factors. The last of these methods measures only preferences, for availability and other environmental influences are cancelled out or equalized. Once conclusions were reached about the food-habits of a given species, they were checked against its structural adaptations for feeding. The resulting data, notwithstanding an expected variation, show a gratifying overall agreement sufficient to warrant the conclusion that food selection can be rather accurately measured through the use of several fairly simple techniques, each of which contributes in its own way to the end result.

SUMMARY AND CONCLUSIONS

1. A detailed survey of food selection in 76 species of Orthoptera (*sens. lat.*) of southeastern Michigan was carried out during the 1953 through 1955 and the 1957 through 1959 seasons. It involved the accumulation of feeding records in the insects' natural habitats, the use of differential feeding tests, the analysis of their crop contents and fecal materials, and the study of the structural adaptations of their mouthparts to foods. The strengths and weaknesses of these techniques are pointed out, and the results are critically reviewed in the light of an extensive literature.

2. Two methods of obtaining feeding records are described. A total of 300 feeding records for 48 species is listed. Descriptions are given of the more important localities at which feeding occurred, and remarks on the relative abundance, hence, availability, of food-plants are included in an appendix.

3. An improved method of carrying out differential feeding tests and of recording their results is given, along with a description of maintenance equipment and techniques. Data are given on tests involving 32 species of non-omnivorous Orthoptera. Omnivorous species were not studied in this manner, for they were considered so unselective as to be unproductive in tests of this type. An unusually large number of plant species, usually 30 to 50 or more, were used in the experiments on each species of Orthoptera, making possible a fairly comprehensive estimate of the total range of food preference of each. A number of the more abundant plants of the stations was also tested repeatedly in the cages of each orthopteran species to assure an accurate estimate of preference value.

4. The effective technique of analyzing crop contents and fecal materials to study food selection is described. Data are given on crop analyses of 58 species and on fecal analyses of 43 species.

5. The suitability of using mouthpart and other structural adaptations of Orthoptera as tools in the diagnosis of food selection is discussed. The technique used in the present study is described. The mouthparts, especially the mandibles, of Michigan Orthoptera are classified, and the distribution of these types in 64 species is given.

6. It is pointed out that feeding is so diversified in the Orthoptera as to defy description and that the only way in which it can be meaningfully discussed consists of examining it in individual families and subfamilies of the order, showing the full range of feeding in each and then generalizing about the habits of the majority. This is done for each of the major groups of Michigan, using data from the present study and reviewing it in the light of an extensive literature. Based on this discussion, the primary and secondary, if any, food-habits of the groups are summarized in Table IV.

7. The food-habits among species of a subfamily are most often rather similar and tend to be unlike those of species belonging to other groups, even related ones. Nevertheless, there may be considerable overlap between the food-habits of different subfamilies.

8. It appears that most groups of Orthoptera are polyphagous, sometimes to the point of omnivory. Only a few isolated species and genera of herbivores are oligophagous or monophagous.

9. The most widespread type of food-habit is the omnivorous, for approximately one-half of the groups studied are either omnivorous or modified omnivorous. These scavengers usually eat whatever is available in the way of dead or decomposing plant and animal materials but often may take living materials. Despite the marked latitude which characterizes their feeding behavior, most omnivores tend to specialize somewhat in one or more major food categories, though capable of selecting more widely. Field crickets, for example, tend toward herbivory, though they eat a wide assortment of both plant and animal materials.

10. The herbivores among the Orthoptera show definite, consistent preferences. They usually specialize in a single category of food, *e.g.*, grasses or forbs, but select widely within the category. A wide variety of plants, including rushes, horsetails, ferns, mosses, lichens, fungi, and algae, and especially forbs, grasses, sedges, and woody trees, vines, and shrubs is taken. All parts of these plants, including roots, stems, and especially leaves and flowers, are eaten.

11. Predation is common in the Orthoptera. The weaker predators, which are not usually voracious, eat many kinds of small, soft-bodied insects. In contrast, the powerful predators, like mantids, show practically no preferences and rapaciously eat almost any insect of suitable size which they can catch and overpower, including members of their own species. Some predators pursue their prey; some stalk it; others lie in wait for it to move close enough for capture. Teneral, injured, or weakened prey are often taken by predacious Orthoptera and sometimes by groups not normally predacious. This latter type of food selection, the eating of weakened prey, is somewhat intermediate between true predation and scavenging.

12. Even a cursory examination of data given in this study reveals that food-habits are probably not suitable for diagnostic use in taxonomic separation of closely related species of Orthoptera, for there is generally too little difference between their food selection. Nevertheless, it is possible that there are instances in which food-habits can be used as indicators of adaptive radiation, though no such case was uncovered in this study.

13. On the basis of the demonstrated latitude of food selection in most groups and species of Orthoptera and in view of the general availability of their common food-plants and prey in most of their habitations, it is concluded that food probably plays only a minor part in the insects' habitat selection. The few monophagous or oligophagous species encountered, species necessarily restricted to areas in which their host plants grow, are doubtlessly exceptions.

14. The results of the investigation are in general agreement with those of the only comparable work, Isely's pioneering studies on Texas Acrididae and Tettigoniidae, but are based on a different fauna and are more comprehensive and much wider in scope, treating representatives of all major groups of Orthoptera of the eastern United States and using certain methods he did not use.

15. The categories of food taken by Orthoptera are classified and discussed. They include (1) plant products, (2) dead plant materials, (3) living plants, (4) animal products, wastes, and secretions, (5) dead animal materials, and (6) living animals. Groups and species of Orthoptera selecting each of these foods are listed.

16. Many Orthoptera accept dead, dried vegetable materials of a type they do not ordinarily eat in the living, green condition. This suggests that some of the specificity that grasshoppers and allies exhibit in their food selection may be lost upon the death and desiccation of their food-plants.

17. It is noted that numerous interrelated factors regulate or, at least, influence food selection in Orthoptera and that these factors are responsible for minor discrepancies in the data of the present investigation. Factors relative to the climate, to the food, and to the feeder are listed. Climate is a modifying agent through changes in heat, light, humidity, and wind, as altered by cover. Food varies in its attractiveness, in its availability, in its size, and in its developmental and physiological condition. The feeder, too, varies in a number of ways which influence the course of its food selection. It varies physiologically in terms of hunger, thirst, injury, disease, and parasitism; developmentally in terms of hatching, size, molting, sexual maturity, and senescence; and in relation to other factors, including habit patterns, conditioning to food, and degree of crowding.

18. In general, the food-habits of different life stages of a given species are found to be similar, though sometimes influenced by seasonal changes in food availability and condition. Developmental changes in size, condition, and habits of the feeder may also alter food selection.

19. The food-habits of the two sexes, like those of different life stages of the same species, are found to be similar.

20. The latitude of food selection in Orthoptera tends to be enhanced under conditions of starvation pressure. Nevertheless, many species willingly starve rather than eat foods different from those which they normally select in nature.

21. Some Orthoptera have great preference for foods, both animal and plant, not normally found in their environments. Lettuce, for example, is almost a universal food for Orthoptera. Only certain seminivores, carnivores, and graminivores reject it.

22. Notwithstanding the complexity of food selection and the pitfalls inherent in the study of it, the data of this investigation show a gratifying overall agreement, which indicates that each of the above techiques of study is valuable and reliable when

used with discretion. Food selection, therefore, can be rather accurately measured through the use of a number of fairly simple methods, each of which contributes in its own way to the end result.

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The literature on food selection in Orthoptera is vast and unwieldy. It is relatively difficult to find, for it usually comprises but incidental parts of larger studies on other subjects, and its papers are widely scattered throughout numerous, often obscure ecologic, economic, taxonomic, and other journals, both private and governmental, in a host of languages. Much of it is repetitious and relates largely to the control of the numerous noxious species in the order, particularly earwigs, cockroaches, crickets, and plague locusts. This segment of the literature, of which the valuable publications of the Anti-Locust Research Centre are an outstanding exception, is sometimes useless as a source of basic information. Nevertheless, the extensiveness of the literature assures the presence of a considerable amount of worthwhile information, providing one can locate it.

On the basis of the foregoing, it is apparent that it is a difficult undertaking to survey the literature dealing with food selection even in a given family, and it is a practical impossibility to do so for the Orthoptera as a whole. Hence, the following bibliography is offered with no pretense of completeness, though it is hoped that it presents a reasonable coverage of the salient literature. It includes only those works cited in this report, which have been examined personally by the author, and represents but a fraction of the total he has perused over the last eight years. It necessarily excludes many valuable studies which duplicate those already cited and presents other less-significant ones which document points developed in the text.

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TABLE I[17]
FEEDING RECORDS TAKEN IN NATURE

Feeder	No. of Feeders	Sex	Food	Part Eaten	Approx. Time	Date	Sta.	Observer
Parcoblatta uhleriana	1	F	Rodent feces		9:30 P.M.	Aug. 10, '55	31	SKG
" "	1	F	Crataegus sp.	Fruit	10:20 P.M.	Aug. 15, '55	31	SKG
Diapheromera femorata	1	F	Tilia americana	Leaf	11:30 P.M.	Aug. 28, '54	8	SKG
" "	1	F	Rubus occidentalis	Leaf	10:45 P.M.	Sept. 29, '54	8	SKG
" "	1	F	Prunus serotina	Leaf	10:30 P.M.	Aug. 9, '55	31	SKG
" "	1	Nymph	Corylus americana	Leaf	9:45 P.M.	July 1, '58	27	SKG
" "	1	Nymph	Quercus velutina	Leaf	10:45 P.M.	July 9, '59	27	SKG
" "	1	M	Quercus rubra	Leaf	9:45 P.M.	July 30, '59	27	SKG
" "	1	?	Lespedeza capitata*	Flower	12:35 P.M.	Aug. 4, '59	27	JKH
" "	1	Nymph	Quercus velutina	Leaf	11:20 P.M.	Aug. 5, '59	27	JKH
" "	1	Nymph	Quercus velutina	Leaf	10:00 P.M.	Aug. 17, '59	27	JKH
Chloealtis conspersa	1	F	Fragaria virginiana	Leaflet (dry)	11:30 A.M.	July 14, '54	13	SKG
" "	2	FF	Danthonia spicata	Leaf (dry)	11:30 A.M.	July 14, '54	13	SKG
" "	1	?	Poa pratensis	Leaf	4:00 P.M.	July 14, '59	27	JKH
Chorthippus longicornis	1	?	Andropogon Gerardi	Leaf	12:10 P.M.	Sept. 1, '53	14	SKG
Orphulella speciosa	1	M	Poa pratensis	Leaf	9:30 A.M.	July 14, '54	12	SKG
Pseudopomala brachyptera	1	Nymph	Agrostis alba	Leaf	11:30 A.M.	July 27, '57	31B	SKG
Syrbula admirabilis	1	Nymph	Aristida purpurascens	Leaf	1:00 P.M.	June 26, '58	27	SKG
Arphia p. pseudonietana	1	F	Poa pratensis	Leaf	4:05 P.M.	Aug. 5, '59	27	JKH
Camnula pellucida	1	F	Poa pratensis	Leaf	11:00 A.M.	July 18, '55	31B	SKG
Chortophaga viridifasciata	1	F	Mentha piperita	Leaf & petiole	3:00 P.M.	May 17, '54	22B	SKG
" "	Same indiv.		Dactylis glomerata	Leaf	3:00 P.M.	May 17, '54	22B	SKG
" "	1	?	Danthonia spicata*	Leaf	11:30 A.M.	May 25, '54	17A	SKG
" "	1	?	Dactylis glomerata	Leaf	9:30 A.M.	June 9, '54	17A	SKG
Dissosteira carolina	1	M	Poa pratensis	Leaf	11:00 A.M.	July 25, '54	12	SKG
" "	1	?	Cirsium arvense	Leaf	1:30 P.M.	Aug. 5, '54	28C	SKG
" "	1	?	Berteroa incana*	Leaf	2:15 P.M.	July 23, '59	27	JKH
" "	1	F	Moss	Leaf	3:30 P.M.	Aug. 11, '59	27	JKH
Encoptolophus s. sordidus	1	F	Poa pratensis	Leaf	3:15 P.M.	Sept. 3, '55	31B	SKG
Spharagemon b. bolli	1	F	Hieracium longipilum	Leaf (dry)	10:00 A.M.	July 16, '59	27	JKH
" " "	1	F	Poa compressa	Leaf (dry)	4:45 P.M.	July 28, '59	27	JKH
" " "	1	M	Moss	Leaf	12:15 M.	Aug. 2, '59	27	JKH
" " "	1	F	Equisetum arvense	Leaf	3:00 P.M.	Aug. 8, '59	27	JKH
Spharagemon collare	1	F	Rumex Acetosella	Leaf (basal)	11:10 A.M.	Sept. 3, '55	31B	SKG
" "	1	M	Poa pratensis	Leaf	12:45 P.M.	Sept. 3, '55	31B	SKG
" "	1	M	Composite sp.	Stem (broken tip)	3:00 P.M.	Sept. 3, '55	31B	SKG

*Nibbled

[17]See p.163 for a discussion of the formulation and use of the following data.

TABLE I (CONT.)
FEEDING RECORDS TAKEN IN NATURE

Feeder	No. of Feeders	Sex	Food	Part Eaten	Approx. Time	Date	Sta.	Observer
Spharagemon collare	1	F	Poa pratensis	Spikelet	10:07 P.M.	July 17, '59	27	JKH
" "	1	F	Penstemon hirsutus	Leaf	5:00 P.M.	July 23, '59	27	JKH
" "	1	M	Lactuca canadensis	Flower head	1:45 P.M.	July 29, '59	27	JKH
Melanoplus b. bilituratus	1	M	Poa pratensis	Leaf	10:30 A.M.	Sept. 3, '55	31B	SKG
" " "	1	M	Solidago nemoralis	Flower head	11:45 A.M.	Sept. 3, '55	31B	SKG
" " "	1	F	Rumex Acetosella	Leaf (basal)	12:45 P.M.	Sept. 3, '55	31B	SKG
" " "	1	?	Moss	Leaf	1:55 P.M.	July 25, '59	27	JKH
" " "	1	?	Rudbeckia serotina	Leaf	2:25 P.M.	July 25, '59	27	JKH
Melanoplus bivittatus	1	F	Mentha arvensis	Leaf	9:30 A.M.	Aug. 31, '53	5	SKG
" "	1	F	Verbena urticifolia	Leaf	11:00 A.M.	Sept. 1, '53	14	SKG
" "	2	FF	Solidago canadensis	Ray flower	11:00 A.M.	Sept. 1, '53	14	SKG
" "	1	Nymph	Solidago canadensis	Ray flower	11:00 A.M.	Sept. 1, '53	14	SKG
" "	1	F	Scirpus atrovirens	Leaf	10:30 P.M.	Sept. 3, '53	5	SKG
" "	Same indiv.		Typha latifolia	Leaf	10:30 P.M.	Sept. 3, '53	5	SKG
" "	2	M,F	Aster puniceus	Flower head	10:15 A.M.	Sept. 16, '53	18	SKG
" "	1	?	Sagittaria latifolia	Leaf	10:00 P.M.	Aug. 2, '54	5	SKG
" "	1	Nymph	Potentilla fruticosa	Leaf & terminal bud	8:45 P.M.	Aug. 13, '53	28D	SKG
" "	1	F	Typha latifolia	Leaf	8:45 P.M.	Aug. 13, '53	28D	SKG
" "	2	?	Phleum pratense	Spikelet	12:30 P.M.	July 2, '58	27	AMW
" "	1	?	Daucus Carota	Leaf	11:40 A.M.	July 14, '59	27	JKH
" "	1	M	Erechtites hieracifolia	Leaf	4:10 P.M.	July 14, '59	27	JKH
" "	1	?	Asclepias syriaca	Flower	7:10 P.M.	July 16, '59	27	JKH
" "	1	F	Asparagus officinalis	Stem	10:35 P.M.	Aug. 12, '59	27	JKH
Melanoplus confusus	2	M,F	Cirsium arvense	Leaf	11:00 A.M.	July 1, '55	31B	SKG
" "	1	M	Monarda fistulosa	Perianth	10:00 A.M.	July 26, '55	31B	SKG
" "	1	M	Asclepias syriaca	Leaf	11:30 A.M.	June 18, '57	31	SKG
" "	1	F	Phleum pratense	Leaf	11:45 A.M.	June 18, '57	31	SKG
" "	1	M	Rumex Acetosella*	Leaf (basal)	12:30 M.	June 19, '57	13	SKG
" "	Same indiv.		Solidago prob. juncea	Leaf (basal)	12:30 M.	June 19, '57	13	SKG
" "	1	M	Cirsium arvense	Leaf	10:20 A.M.	July 5, '57	31B	SKG
" "	1	F	Carya glabra	Leaf (dried)	9:30 A.M.	June 18, '58	27	SKG
" "	1	F	Acheta pennsylvanicus	Body (dried)	12:15 M.	June 19, '58	27	SKG
" "	1	F	Setaria glauca	Leaf	4:00 P.M.	July 20, '59	27	JKH
" "	1	?	Poa pratensis	Leaf (dried)	4:00 P.M.	July 29, '59	27	JKH

*Nibbled

TABLE I (CONT.)
FEEDING RECORDS TAKEN IN NATURE

Feeder	No. of Feeders	Sex	Food	Part Eaten	Approx. Time	Date	Sta.	Observer
Melanoplus f.-r. f.-r.	1	F	Cichorium Intybus	Flower head	11:00 A.M.	Aug. 31, '53	6	SKG
" " "	Same indiv.		Ambrosia artemisiifol.	Flower head	11:00 A.M.	Aug. 31, '53	6	SKG
" " "	1	F	Trifolium sp.	Leaflet	11:00 A.M.	Aug. 31, '53	6	SKG
" " "	1	?	Typha latifolia	Leaf	10:30 P.M.	Sept. 3, '53	5	SKG
" " "	1	M	Plantago Rugelii*	Leaf	10:30 P.M.	July 19, '54	12	SKG
" " "	1	Nymph	Solidago canadensis	Leaf (dry)	11:30 A.M.	Aug. 9, '54	21A	SKG
" " "	1	?	Dactylis glomerata	Leaf	2:30 P.M.	Aug. 25, '54	12	SKG
" " "	1	?	Trifolium pratense	Leaflet	2:30 P.M.	Aug. 25, '54	12	SKG
" " "	1	Nymph	Dactylis glomerata	Leaf	2:30 P.M.	Aug. 25, '54	12	SKG
" " "	1	?	Aster lateriflorus	Flower bud	11:45 P.M.	Aug. 28, '54	13	SKG
" " "	1	?	Solidago graminifolia	Flower head	10:00 P.M.	Sept. 3, '54	25	SKG
" " "	1	?	Scirpus validus	Spike	10:00 P.M.	Sept. 3, '54	25	SKG
" " "	1	?	Aster lateriflorus	Leaf	10:00 P.M.	Sept. 3, '54	25	SKG
" " "	1	Nymph	Cirsium arvense	Leaf	11:00 A.M.	July 26, '55	31B	SKG
" " "	1	Nymph	Monarda fistulosa	Perianth	3:30 P.M.	July 29, '55	31B	SKG
" " "	1	Nymph	Monarda fistulosa	Leaf	10:28 P.M.	July 30, '59	27	SKG
" " "	1	Nymph	Monarda fistulosa	Leaf	10:35 P.M.	July 30, '59	27	SKG
" " "	1	Nymph	Desmodium paniculatum	Flower	10:45 P.M.	July 30, '59	27	SKG
" " "	1	Nymph	Solidago juncea	Flower head	11:10 P.M.	July 31, '59	27	JKH
" " "	1	M	Asclepias syriaca	Leaf	10:30 P.M.	Aug. 11, '59	27	JKH
" " "	1	F	Asclepias syriaca	Leaf	10:25 P.M.	Aug. 12, '59	27	JKH
" " "	1	M	Monarda fistulosa	Leaf	12:00 P.M.	Aug. 12, '59	27	JKH
" " "	1	F	Berteroa incana	Fruit	10:15 P.M.	Aug. 13, '59	27	JKH
" " "	1	M	Verbascum Thapsus	Flower (unopened)	10:25 P.M.	Aug. 13, '59	27	JKH
" " "	1	M	Asclepias syriaca	Flower (dry)	11:45 P.M.	Aug. 14, '59	27	JKH
" " "	1	M	Asclepias syriaca	Fruit	11:45 P.M.	Aug. 15, '59	27	JKH
" " "	1	F	Monarda fistulosa	Leaf	10:20 P.M.	Aug. 22, '59	27	JKH
Melanoplus f.-r. f.-r. (?)	1	Nymph	Phleum pratense	Spikelet & leaf	11:00 P.M.	July 1, '55	31B	SKG
Melanoplus keeleri luridus	1	F	Solidago canadensis	Leaf	10:00 A.M.	Aug. 3, '55	14	SKG
" " "	1	M	Solidago juncea	Leaf	3:45 P.M.	Nov. 14, '58	28	SKG
" " "	1	?	Erigeron strigosus	Leaf	4:20 P.M.	July 23, '59	27	JKH
" " "	1	?	Monarda fistulosa	Leaf	4:10 P.M.	July 27, '59	27	JKH
" " "	1	?	Monarda fistulosa	Leaf	4:40 P.M.	July 27, '59	27	JKH

*Nibbled

TABLE I (CONT.)
FEEDING RECORDS TAKEN IN NATURE

Feeder	No. of Feeders	Sex	Food	Part Eaten	Approx. Time	Date	Sta.	Observer
Melanoplus s. scudderi	1	F	Melilotus alba	Flower & stalk	9:30 A.M.	Sept. 3, '53	15	SKG
" " "	1	?	Plantago sp.*	Leaf	2:30 P.M.	Sept. 1, '54	13	SKG
Melanoplus sp.	1	Nymph	Phleum pratense	Leaf	10:00 A.M.	July 19, '57	31B	SKG
" "	1	Nymph	Monarda fistulosa	Leaf	10:30 A.M.	July 19, '57	31B	SKG
" "	1	Nymph	Cirsium arvense	Leaf	10:40 A.M.	July 27, '57	31B	SKG
" "	1	Nymph	Phleum pratense	Leaf	10:42 A.M.	July 27, '57	31B	SKG
" "	1	Nymph	Melanoplus b. bilit-uratus (dead)	Gular region	1:00 P.M.	July 27, '57	28B	SKG
" "	1	Nymph	Verbascum Thapsus	Flower	10:30 P.M.	July 17, '59	27	JKH
" "	1	Nymph	Poa compressa	Spikelet	10:31 P.M.	July 17, '59	27	JKH
" "	3	Nymphs	Berteroa incana	Fruit	10:35 P.M.	July 17, '59	27	JKH
" "	1	Nymph	Rudbeckia serotina	Flower head	10:45 P.M.	July 17, '59	27	JKH
" "	1	Nymph	Achillea Millefolium	Leaf	3:15 P.M.	July 29, '59	27	JKH
" "	1	M	Melanoplus sp. F	Wings (while F struggled)	4:50 P.M.	Aug. 5, '59	27	JKH
" "	3	Nymphs	Monarda fistulosa	Leaf & flower	12:15 P.M.	Aug. 12, '59	27	JKH
" "	2	Nymphs	Desmodium paniculatum	Leaf & flower	12:20 P.M.	Aug. 12, '59	27	JKH
" "	1	F	Cirsium vulgare	Flower head	10:20 P.M.	Aug. 17, '59	27	JKH
Schistocerca lineata	1	F	Rumex Acetosella*	Leaf (basal)	3:00 P.M.	Oct. 6, '54	27	SKG
" "	1	Nymph	Lespedeza capitata	Leaflet	11:00 P.M.	Aug. 9, '55	31B	SKG
" "	1	Nymph	Equisetum arvense	Leaf	3:05 P.M.	July 25, '59	27	JKH
" "	1	Nymph	Lespedeza hirta	Perianth	11:30 P.M.	July 28, '59	27	JKH
" "	1	F	Poa pratensis	Leaf (dry)	3:15 P.M.	Aug. 12, '59	27	JKH
" "	Same indiv.		Erigeron strigosus	Leaf (dry)	3:25 P.M.	Aug. 12, '59	27	JKH
" "	1	F	Desmodium paniculatum	Leaflet	11:10 P.M.	Aug. 16, '59	27	JKH
" "	1	F	Moss	Leaf	3:05 P.M.	Aug. 18, '59	27	JKH
" "	1	F	Rubus sp.	Leaflet	11:45 P.M.	Aug. 20, '59	27	JKH
Ceuthophilus brevipes	1	F	Lumbricus terrestris	Body (dry)	9:30 P.M.	Sept. 21, '55	36	DCE
Ceuthophilus pallidipes	1	?	Bracket fungus	Fruiting body	10:30 P.M.	Sept. 20, '55	37	DCE
" "	1	?	Leaf mold	Hyphae	10:30 P.M.	Sept. 20, '55	37	DCE
Ceuthophilus thomasi	1	F	Tsuga canadensis	Cone (green)	11:30 P.M.	Aug. 27, '55	38	DCE
Ceuthophilus uhleri	2	M,F	Magicicada sp.	Body	8:45 P.M.	Aug. 26, '55	39	DCE
Amblycorypha oblongifolia	1	F	Solidago canadensis	Leaf	11:00 P.M.	Aug. 18, '54	8	SKG
" "	1	?	Impatiens capensis	Leaf	11:00 P.M.	Aug. 28, '54	8	SKG
" "	1	?	Solidago canadensis	Leaf	11:00 P.M.	Aug. 28, '54	8	SKG
" "	1	?	Solidago canadensis	Flower head	9:45 P.M.	Sept. 8, '54	8	SKG
" "	1	?	Solidago canadensis	Leaf	9:45 P.M.	Sept. 8, '54	8	SKG

TABLE I (CONT.)
FEEDING RECORDS TAKEN IN NATURE

Feeder	No. of Feeders	Sex	Food	Part Eaten	Approx. Time	Date	Sta.	Observer
Amblycorypha oblongifolia	1	?	Vitis riparia	Leaf	9:45 P.M.	Sept. 8, '54	8	SKG
" "	1	?	Monarda fistulosa	Leaf	9:45 P.M.	Sept. 8, '54	8	SKG
" "	1	?	Rubus occidentalis	Leaf	9:45 P.M.	Sept. 8, '54	8	SKG
" "	1	M	Solidago canadensis	Flower head	11:00 P.M.	Sept. 19, '54	8	SKG
" "	1	?	Solidago canadensis	Flower head	10:00 P.M.	Aug. 11, '55	8	SKG
Amblycorypha rotundifolia	1	M	Collinsonia canaden.	Leaf	10:00 P.M.	Aug. 28, '53	11	SKG
" "	Same indiv.		Collinsonia canaden.	Flower & stalk	10:00 P.M.	Aug. 28, '53	11	SKG
" "	1	?	Solidago canadensis	Leaf	11:00 P.M.	Aug. 28, '54	8	SKG
" "	1	Nymph	Rubus flagellaris	Leaf (dry)	9:40 P.M.	June 18, '58	27	AMW
Scudderia c. curvicauda	1	F	Typha latifolia	Leaf	10:00 P.M.	Aug. 2, '54	5	SKG
" " "	1	?	Asparagus officinalis	Leaf	11:30 P.M.	Aug. 28, '54	13	SKG
" " "	1	Nymph	Carya glabra	Gall on leaf	12:30 M.	June 24, '55	27	SKG
" " "	1	Nymph	Asclepias syriaca	Leaf (dry)	11:00 A.M.	July 1, '55	31B	SKG
" " "	1	F	Typha latifolia	Leaf	10:45 P.M.	Aug. 12, '55	28D	SKG
" " "	1	F	Impatiens capensis	Flower (unopened)	10:45 P.M.	Aug. 12, '55	28D	SKG
" " "	2	FF	Apocynum androsaem.	Flower & stalk	9:50 P.M.	June 30, '59	27	SKG
" " "	1	Nymph	Rubus sp.	Leaf	12:30 P.M.	July 10, '59	27	JKH
" " "	1	Nymph	Asclepias syriaca	Flower (unopened)	12:35 P.M.	July 10, '59	27	JKH
" " "	1	Nymph	Asclepias syriaca	Flower bud	11:50 A.M.	July 14, '59	27	JKH
" " "	1	F	Carex tribuloides	Leaf (dry)	12:00 M.	July 14, '59	27	JKH
" " "	1	?	Asclepias syriaca	Leaf	4:15 P.M.	July 16, '59	27	JKH
" " "	1	Nymph	Asclepias syriaca	Leaf	12:30 P.M.	July 17, '59	27	SKG
" " "	1	F	Verbascum Thapsus	Flower	10:23 P.M.	July 30, '59	27	SKG
" " "	1	F	Asclepias tuberosa	Leaf	11:30 P.M.	Aug. 14, '59	27	JKH
" " "	1	?	Asclepias syriaca	Leaf	12:20 P.M.	Aug. 20, '59	27	JKH
Scudderia f. furcata	1	?	Aster sagittifolius	Flower head	4:00 P.M.	Sept. 10, '53	17A	SKG
" " "	1	F	Rhamnus alnifolia	Leaf	9:30 P.M.	Aug. 9, '54	13	SKG
" " "	1	Nymph	Betula pumila	Leaf (dry)	3:00 P.M.	Aug. 12, '54	28D	SKG
" " "	1	?	Aster sagittifolius	Flower head	11:30 P.M.	Aug. 28, '54	13	SKG
" " "	1	Nymph	Monarda fistulosa	Perianth	9:30 A.M.	July 18, '55	31	SKG
" " "	1	F	Impatiens capensis	Flower	8:30 P.M.	Aug. 13, '55	28D	SKG
" " "	1	F	Impatiens capensis	Fruit	9:00 P.M.	Aug. 13, '55	28D	SKG
" " "	1	M	Polymnia canadensis	Leaf	8:30 P.M.	Aug. 13, '55	35	DCE
" " "	1	M	Rhus typhina	Leaflet	10:30 P.M.	Aug. 23, '55	8	SKG
" " "	1	Nymph	Asclepias syriaca	Flower (dry)	11:50 P.M.	July 16, '59	27	SKG
" " "	1	Nymph	Asclepias syriaca	Leaf (dry)	11:30 P.M.	July 24, '59	27	SKG
" " "	1	Nymph	Asclepias syriaca	Leaf (dry)	10:50 P.M.	July 28, '59	27	JKH

TABLE I (CONT.)
FEEDING RECORDS TAKEN IN NATURE

Feeder	No. of Feeders	Sex	Food	Part Eaten	Approx. Time	Date	Sta.	Observer
Scudderia f. furcata	1	Nymph	Asclepias syriaca	Flower	10:10 P.M.	July 30, '59	27	SKG
Scudderia texensis	1	M	Verbascum Thapsus	Flower	10:55 P.M.	July 17, '59	27	JKH
" "	1	F	Cornus racemosa	Leaf	11:30 A.M.	July 27, '59	27	JKH
Scudderia sp.	1	?	Verbascum Thapsus	Flower	10:50 P.M.	Aug. 12, '59	27	JKH
" "	1	Nymph	Rubus sp.	Leaf	12:30 P.M.	Aug. 17, '59	27	JKH
Neoconocephalus ensiger	1	F	Andropogon Gerardi	Grain	11:30 P.M.	Sept. 11, '53	17B	SKG
" "	1	M	Agrostis alba	Grain (dry)	10:30 P.M.	Aug. 1, '54	13	SKG
" "	1	M	Plantago Rugelii	Fruit	11:30 P.M.	Aug. 28, '54	13	SKG
" "	2	MM	Setaria glauca	Grain	11:30 P.M.	Aug. 28, '54	13	SKG
" "	1	M	Rumex crispus	Fruit (dry)	10:30 P.M.	Sept. 3, '54	25	SKG
" "	1	F	Phleum pratense	Grain (dry)	1:00 A.M.	Aug. 10, '55	31B	SKG
" "	1	M	Setaria glauca	Grain	9:30 P.M.	Sept. 17, '58	13	SKG
Conocephalus attenuatus	20+	MM, FF	Eupatorium perfoliat.	Flower head	11:00 P.M.	Aug. 23, '54	29	SKG
" "	1	?	Scirpus atrovirens	Spike	11:00 P.M.	Aug. 23, '54	29	SKG
" "	1	?	Juncus effusus	Fruit	11:00 P.M.	Aug. 23, '54	29	SKG
" "	20+	MM, FF	Eupatorium perfoliat.	Flower head	9:30 P.M.	Sept. 1, '54	29	SKG
Conocephalus brevipennis	1	M	Leersia oryzoides	Leaf sheath	10:00 P.M.	Sept. 3, '53	5	SKG
" "	4	?	Leersia oryzoides	Spikelet	10:00 P.M.	Sept. 3, '53	5	SKG
" "	1	?	Leersia oryzoides	Leaf & sheath	10:00 P.M.	Sept. 3, '53	5	SKG
" "	1	?	Typha latifolia	Fruit	10:00 P.M.	Sept. 3, '53	5	SKG
" "	1	F	Aster laevis	Flower head	3:00 P.M.	Sept. 9, '53	4A	SKG
" "	1	Nymph	Sagittaria latifolia	Leaf	10:00 P.M.	Aug. 2, '54	5	SKG
" "	1	?	Agrostis alba	Spikelet	11:30 P.M.	Aug. 28, '54	13	SKG
" "	1	?	Setaria glauca	Spikelet	11:30 P.M.	Aug. 28, '54	13	SKG
" "	1	?	Panicum lanuginosum	Spikelet	11:30 P.M.	Aug. 28, '54	13	SKG
" "	2	?	Solidago canadensis	Flower head	10:00 P.M.	Sept. 3, '54	25	SKG
" "	2	?	Juncus tenuis	Fruit	10:00 P.M.	Sept. 3, '54	25	SKG
" "	2	?	Juncus Torreyi	Fruit	10:00 P.M.	Sept. 3, '54	25	SKG
" "	3	?	Scirpus atrovirens	Spike	10:00 P.M.	Sept. 3, '54	25	SKG
" "	1	?	Scirpus validus	Spike	10:00 P.M.	Sept. 3, '54	25	SKG
" "	4	?	Leersia oryzoides	Spikelet	10:00 P.M.	Sept. 3, '54	25	SKG
" "	1	?	Mimulus ringens	Flower	10:00 P.M.	Sept. 3, '54	25	SKG
" "	1	?	Vernonia altissima	Flower head	10:00 P.M.	Sept. 3, '54	25	SKG
" "	1	M	Muhlenbergia Schreberi	Spikelet	11:30 P.M.	Sept. 19, '54	8	SKG
" "	1	?	Chrysops sp.	Head & abdomen	10:30 A.M.	July 18, '55	31B	SKG
" "	1	M	Phleum pratense	Spikelet (dry)	1:00 A.M.	Aug. 10, '55	31B	SKG
" "	1	F	Impatiens capensis	Fruit	8:30 P.M.	Aug. 13, '55	28D	SKG

TABLE I (CONT.)
FEEDING RECORDS TAKEN IN NATURE

Feeder	No. of Feeders	Sex	Food	Part Eaten	Approx. Time	Date	Sta.	Observer
Conocephalus brevipennis	1	Nymph	Andropogon Gerardi	Spikelet	1:30 A.M.	Aug. 14, '55	28D	SKG
" "	1	M	Impatiens capensis	Flower	2:00 A.M.	Aug. 14, '55	28D	SKG
Conocephalus brevipennis (?)	1	Nymph	Plantago lanceolata*	Perianth	11:00 A.M.	July 25, '54	12	SKG
" "	1	Nymph	Dipteran larva	Body (dry)	11:00 A.M.	July 25, '54	12	SKG
Conocephalus f. fasciatus	20+	MM,FF	Agrostis alba	Spikelet	10:30 P.M.	Aug. 2, '54	25	SKG
" " "	1	?	Impatiens capensis	Flower	11:00 P.M.	Aug. 23, '54	29	SKG
" " "	20+	MM,FF	Eupatorium perfoliat.	Flower head	11:00 P.M.	Aug. 23, '54	29	SKG
" " "	5	?	Eupatorium perfoliat.	Flower head	9:30 P.M.	Sept. 1, '54	29	SKG
" " "	1	F	Agrostis alba	Spikelet	10:30 P.M.	Sept. 3, '54	25	SKG
Conocephalus nigropleurum	1	M	Eupatorium perfoliat.	Flower head	10:15 A.M.	Sept. 16, '53	18	SKG
" "	1	F	Impatiens capensis	Flower	1:30 A.M.	Aug. 10, '55	28D	SKG
Conocephalus strictus	7	?	Setaria glauca	Spikelet	11:30 P.M.	Aug. 28, '54	13	SKG
" "	1	F	Phleum pratense	Spikelet (dry)	1:00 A.M.	Aug. 10, '55	31B	SKG
" "	2	M,F	Phleum pratense	Spikelet (dry)	10:30 P.M.	Aug. 10, '55	31B	SKG
" "	1	Nymph	Achillea Millefolium	Inflorescence	11:05 P.M.	July 17, '59	27	JKH
" "	1	?	Poa compressa	Spikelet (dry)	2:15 P.M.	July 28, '59	27	JKH
" "	Same indiv.		Rumex Acetosella	Flower (dry)	2:15 P.M.	July 28, '59	27	JKH
" "	1	Nymph	Verbascum Thapsus	Flower	11:15 P.M.	July 28, '59	27	JKH
" "	1	Nymph	Potentilla intermedia	Flower	11:20 P.M.	July 28, '59	27	JKH
" "	1	Nymph	Achillea Millefolium	Flower head	10:00 P.M.	July 30, '59	27	SKG
" "	1	Nymph	Mosquito	Entire body (taken in mid-air)	10:50 P.M.	July 30, '59	27	SKG
" "	1	Nymph	Rudbeckia serotina	Flower head	11:34 P.M.	July 30, '59	27	SKG
" "	1	F	Poa compressa	Spikelet	4:20 P.M.	Aug. 5, '59	27	JKH
" "	1	Nymph	Monarda fistulosa	Flower	10:25 P.M.	Aug. 5, '59	27	JKH
" "	1	Nymph	Ant	Entire body (while ant struggled)	3:20 P.M.	Aug. 8, '59	27	JKH
" "	1	M	Poa compressa	Spikelet	10:05 P.M.	Aug. 12, '59	27	JKH
" "	1	?	Asclepias syriaca	Leaf (dry)	11:40 P.M.	Aug. 14, '59	27	SKG
" "	1	Nymph	Undetermined insect	Entire body (captured in mid-air)	11:30 P.M.	Aug. 17, '59	27	JKH
" "	1	F	Moss	Leaf	3:00 P.M.	Aug. 18, '59	27	JKH
" "	1	F	Poa compressa	Spikelet	3:15 P.M.	Aug. 18, '59	27	JKH
" "	1	F	Poa compressa	Spikelet	9:35 P.M.	Aug. 19, '59	27	SKG
" "	1	F	Lespedeza capitata	Leaflet	9:15 P.M.	Aug. 22, '59	27	JKH
" "	1	Nymph	Achillea Millefolium	Flower head	9:40 P.M.	Aug. 22, '59	27	JKH
Conocephalus sp.	1	Nymph	Impatiens capensis	Flower	10:45 P.M.	Aug. 12, '55	28D	SKG
Orchelimum gladiator	1	M	Carex stricta var. strictior	Leaf	10:30 A.M.	July 8, '54	25	SKG
" "	1	M	Eleocharis calva	Spike	10:00 A.M.	July 15, '54	25	SKG

*Nibbled

TABLE I (CONT.)
FEEDING RECORDS TAKEN IN NATURE

Feeder	No. of Feeders	Sex	Food	Part Eaten	Approx. Time	Date	Sta.	Observer
Orchelimum gladiator	1	M	Betula pumila	Fruit	3:00 P.M.	Aug. 19, '54	28D	SKG
Orchelimum nigripes	1	M	Typha latifolia	Fruit	10:30 P.M.	Sept. 3, '53	5	SKG
" "	2	FF	Typha latifolia	Fruit	10:30 P.M.	Sept. 3, '53	5	SKG
Orchelimum volantum	1	M	Carex comosa	Leaf (dry)	9:45 P.M.	Sept. 1, '54	29	SKG
Orchelimum vulgare	1	M	Carex vulpinoidea	Spike	1:15 A.M.	July 22, '59	27	JKH
Orchelimum sp.	1	?	Achillea Millefolium	Flower head	11:30 P.M.	Aug. 3, '59	27	JKH
" "	1	M	Poa compressa	Spikelet	12:05 P.M.	Aug. 17, '59	27	JKH
Acheta pennsylvanicus	1	F	Mucous		9:45 A.M.	Sept. 20, '57	40	SKG
" "	1	F	Melanoplus confusus	Leg	4:15 P.M.	June 18, '58	27	SKG
" "	1	?	Quercus sp.	Ament	3:45 P.M.	June 22, '58	8	SKG
" "	1	Nymph	Atlanticus testaceus	Abdomen (injured prey)	1:30 A.M.	July 12, '59	27	JKH
" "	1	M	Poa pratensis	Spikelet	10:45 P.M.	July 15, '59	27	JKH
Nemobius allardi	1	?	Daucus Carota*	Flower head	3:00 P.M.	Aug. 25, '54	12	SKG
Neoxabea bipunctata	2	FF	Polymnia canadensis	Flower head	8:30 P.M.	Aug. 13, '55	35	DCE
Oecanthus angustipennis	1	M	Polymnia canadensis	Flower head	8:30 P.M.	Aug. 13, '55	35	DCE
" "	1	?	Lactuca biennis	Flower head	10:00 P.M.	Sept. 5, '53	16	SKG
Oecanthus n. nigricornis	1	M	Monarda fistulosa	Flower (dry)	10:30 P.M.	Sept. 1, '53	10	SKG
" " "	1	M	Solidago canadensis	Flower head	10:30 P.M.	Sept. 1, '53	10	SKG
Oecanthus n. quadripunctatus	1	?	Solidago nemoralis	Flower head	10:00 P.M.	Sept. 5, '53	16	SKG
" " "	1	F	Aphids on Desmodium sessilifolium	Entire body	1:00 A.M.	Aug. 10, '55	31B	SKG
" " "	1	Nymph	Verbascum Thapsus	Flower	12:50 P.M.	July 8, '59	27	JKH
" " "	1	Nymph	Asclepias syriaca	Flower bud	1:30 A.M.	July 10, '59	27	JKH
" " "	1	Nymph	Verbascum Thapsus	Flower	11:45 P.M.	July 15, '59	27	JKH
" " "	1	Nymph	Asclepias syriaca	Fruit	12:15 P.M.	July 17, '59	27	SKG
" " "	1	Nymph	Verbascum Thapsus	Flower	11:15 P.M.	July 18, '59	27	JKH
" " "	1	Nymph	Verbascum Thapsus	Flower	11:10 P.M.	July 20, '59	27	JKH
" " "	1	Nymph	Verbascum Thapsus	Flower	11:30 P.M.	July 20, '59	27	JKH
" " "	1	Nymph	Monarda fistulosa*	Flower	12:00 P.M.	July 21, '59	27	JKH
" " "	1	Nymph	Asclepias syriaca*	Flower (dry)	12:45 P.M.	July 21, '59	27	JKH
" " "	1	M	Asclepias syriaca	Leaf	11:50 P.M.	July 24, '59	27	SKG
" " "	1	F	Monarda fistulosa*	Flower	11:00 P.M.	July 26, '59	27	JKH
" " "	Same indiv.		Monarda fistulosa	Flower	11:15 P.M.	July 26, '59	27	JKH
" " "	1	M	Asclepias syriaca	Leaf	11:30 P.M.	July 26, '59	27	JKH
" " "	1	Nymph	Verbascum Thapsus	Flower	11:10 P.M.	July 28, '59	27	JKH
" " "	1	Nymph	Solidago speciosa	Leaf (dry)	11:35 P.M.	July 28, '59	27	JKH
" " "	1	Nymph	Rubus flagellaris	Leaflet (dry)	9:35 P.M.	July 30, '59	27	SKG

*Nibbled

TABLE I (CONT.)
FEEDING RECORDS TAKEN IN NATURE

Feeder	No. of Feeders	Sex	Food	Part Eaten	Approx. Time	Date	Sta.	Observer
Oecanthus n. quadripunctatus	1	F	Achillea Millefolium	Flower head	10:18 P.M.	July 30, '59	27	SKG
" " "	1	Nymph	Desmodium paniculatum	Flower	10:47 P.M.	July 30, '59	27	SKG
" " "	1	F	Vernonia altissima	Flower head	11:00 P.M.	July 30, '59	27	SKG
" " "	2	?	Verbascum Thapsus	Flower	11:00 P.M.	July 31, '59	27	JKH
" " "	1	F	Desmodium paniculatum	Flower	11:45 P.M.	Aug. 3, '59	27	JKH
" " "	1	?	Vernonia sp.	Flower head	12:15 P.M.	Aug. 4, '59	27	JKH
" " "	2	M,F	Erigeron strigosus	Flower head	11:05 P.M.	Aug. 5, '59	27	JKH
" " "	1	Nymph	Lespedeza capitata	Flower	10:15 P.M.	Aug. 8, '59	27	JKH
" " "	1	M	Monarda fistulosa	Flower	10:35 P.M.	Aug. 8, '59	27	JKH
" " "	1	M	Asclepias syriaca	Leaf	10:50 P.M.	Aug. 8, '59	27	JKH
" " "	1	?	Erigeron canadensis	Fruit	10:45 P.M.	Aug. 11, '59	27	JKH
" " "	1	M	Asclepias syriaca	Leaf	9:55 P.M.	Aug. 12, '59	27	JKH
" " "	1	Nymph	Asparagus officinalis	Stem (bark)	10:40 P.M.	Aug. 16, '59	27	JKH
Oecanthus niveus	2	Nymphs	Lychnis alba	Petal	11:00 P.M.	July 28, '54	8	SKG
" "	1	F	Lonicera tatarica	Leaf (dry)	10:30 P.M.	Aug. 9, '54	13	SKG
Anaxipha exigua	1	F	Polymnia canadensis	Flower head	8:30 P.M.	Aug. 13, '55	35	DCE

[17]Table I gives full data on all feeding records obtained during this study. The words same individual appear in place of the data normally recorded under number and sex when the same individual fed on two or more plants during one observation. Either a question mark or the word nymph may also be used in this column in cases when the sex of the feeding individual was not noted or the insect was immature. An asterisk is appended to the name of the food when it was nibbled rather than eaten; nibbling is here defined as feeding for a time so short as to result in negligible damage to the food. The time of feeding indicated is approximate. The abbreviation M., listed in the time column, refers to a time during the noon hour. A total of 27 feeding records for Arphia sulphurea and 39 for Atlanticus testaceus have been withheld but will be presented in later papers. All doubtful records have been deleted from the above. The observers of feeding records are indicated by their initials. These persons include the author, S.K. Gangwere, who personally amassed approximately two-thirds of the records; D.C. Eades, who contributed several feeding records; J.K. Hiltunen, the author's full-time research assistant during the 1959 season, who amassed more than one-fourth of the records; and A.M. Wenner, who was the author's research assistant during the 1958 season.

The following example will illustrate the way in which data provided in Table I may be evaluated in terms of food availability. In Table I it is noted that over forty individuals of Conocephalus attenuatus were observed feeding on Eupatorium perfoliatum, one on Scirpus atrovirens, and one on Juncus effusus. By turning to the lists of relative abundance of plant species provided in Appendix B, it is seen that the first of these food-plants, Eupatorium, is common, but not abundant, at Station 29, the site of these particular feeding

TABLE I (CONT.)
FEEDING RECORDS TAKEN IN NATURE

records. Thus, the marked preference of Conocephalus for this plant is significant, though probably dependent in part on a change in the plant's seasonal condition; often, when plants newly flower, they are unusually attractive to certain feeders. Juncus effusus, an abundant plant at Station 29, was chosen but once, contrasting sharply with Eupatorium, indicating that its preference value is low. The Scirpus record may or may not be significant, for this plant was not abundant enough to have been recorded when the list of plants was made. Nevertheless, by virtue of its comparative scarcity at Station 29, it cannot be a major factor in the diet of Conocephalus, even if its preference value happens to be high.

TABLE II[18]
RESULTS OF DIFFERENTIAL FEEDING TESTS

1. Diapheromera femorata
(Tested early September to middle October)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 67V[19] / 79V / Untouched: 60, 61, 109, 110, 111, 118, 146, 161, 175
Test II. 67V / 112VN[20] / Untouched: 63, 68, 79, 84, 104, 105, 109, 119
Test III. 67V / 63V / 58V / Untouched: 51, 55, 66, 84, 119
Test IV. 66V / 86V / 79V / 112VN & 68VN / Untouched: 84, 105, 146
Test V. 86V / 67V / 119V / Untouched: 109, 123
Test VI. 86V / 62V / 112V / 68V / Untouched: 109, 146
Test VII. 86V / 65VN / 67VN
Test VIII. 63V / 86VN

B. Summary of Relative Preference Value of Frequently Tested Foods:

Rubus occidentalis V 4:1[21] / Quercus velutina V 4:1 / Hamamelis virginiana V 2:1 / Tilia americana V 1:2 / Ulmus rubra V 1:2 & Cornus stolonifera V 1:2

2. Chloealtis conspersa
(Tested early July to early August)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 27VF[22] / 17VF / 29VF / 24F / 162FN / 97FN / Untouched: 74, 76, 114, 148, 165, 174
Test II. 10VF / 17V / 29VF / 27VF / 25F / 45V / 100VN / 99FN / Untouched: 81, 95, 117, 142, 144, 148, 174, 182
Test III. 14V / 16V / 28F / 45V & 29F / 176VN & 96VN / Untouched: 48, 95, 113, 134, 142, 148, 162, 165
Test IV. 14V / 16V / 28VF / 29VF / 45V / 162VN / Untouched: 48, 95, 96, 113, 134, 142, 148, 165, 176
Test V. 16V / 14VF / 10V / 29VF / 28VF / Untouched: 48, 96, 134, 148, 162, 165, 176, 178

[18] See pp184-186for a discussion of the formulation and use of the following data.

[19] 67, as seen in Appendix C (Plants Used In Study), refers to Quercus velutina, while V refers to eating of vegetative parts.

[20] N refers to nibbling rather than eating.

[21] 4:1 is the ratio of acceptances to rejections or nibbling.

[22] F refers to eating of floral parts.

TABLE II (CONT.)
RESULTS OF DIFFERENTIAL FEEDING TESTS

Test VI. 27VF & 17V & 45VF & 29VF / 99V / 81VN / Untouched: 49, 89, 98, 135, 144, 148, 178
Test VII. 29VF & 27VF / 17VF / 45V/Untouched: 49, 81, 144, 148, 174, 176, 178
Test VIII. 29VF & 27V / 45V / 17V / 174VFN / Untouched: 86, 99, 117, 134, 135, 144, 148, 162, 165
Test IX. 29VF & 45V / 17V / 24V / Untouched: 89, 117, 135, 144, 148, 149, 174, 179
Test X. 10VF / 16V / Untouched: 89, 96, 115, 117, 134, 149, 165, 168, 178, 181
Test XI. 16VF / 17VF / 45V / Untouched: 49, 117, 135, 165, 174, 178
Test XII. 16V / 14V & 10V / 28VF / Untouched: 49, 117, 135, 165, 174
Test XIII. 31V / 29V / 28VF / Untouched: 4, 17, 63, 134, 159
Test XIV. 31V & 29V / 28VF / Untouched: 4, 17, 63, 134, 159
Test XV. 31V & 28VF & 17V / Untouched: 63, 134, 159
Test XVI. 29V / 31V / 28VF / 17V / Untouched: 4, 63, 134
Test XVII. 29V / 31V / 28VF / Untouched: 4, 17, 63, 134, 159

B. Summary of Relative Preference Value of Frequently Tested Foods:

Dactylis glomerata V 6:0 / Poa pratensis VF 12:0 & Phleum pratense VF 6:0 & Carex communis V 5:0 / Poa compressa VF 9:0 / Juncus tenuis V 8:0 & Danthonia spicata V 9:3 / Chrysanthemum Leucanthemum VF 0:5 & Rudbeckia serotina VF 0:7

3. Chorthippus longicornis
(Tested middle September to early October)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 33V / 16V / 17V & 28V / 12V / 138VFN & 117FN & 30VN / 21FN & 159VFN & 153FN / Untouched: 81, 111, 113, 144, 148, 168, 179
Test II. 35V / 15V / 7V / Untouched: 59, 82, 87, 108, 109, 159, 160
Test III. 16V / 28V / 19V & 14V / Untouched: 95, 119, 134, 149, 153, 159, 176
Test IV. 16V / 28VF / 6V / Untouched: 1, 93, 148, 153, 168, 176, 178, 179
Test V. 17V / 16V & 33V / 21F / Untouched: 48
Test VI. 39V / 22V & 38VF & 34V / 7VN / 46VN / Untouched: 41, 72, 154, 156, 167
Test VII. 17V & 33V & 16V / 21FN
Test VIII. 14V & 16V / 28V / 12VN

B. Summary of Relative Preference Value of Frequently Tested Foods:

Carex pennsylvanica V 3:0 & Dactylis glomerata V 6:0 & Danthonia spicata V 3:0 / Poa compressa V 4:0 / Eragrostis spectabilis F 1:2 / Aster laevis F 0:3 & Aster sagittifolius VF 0:3

TABLE II (CONT.)
RESULTS OF DIFFERENTIAL FEEDING TESTS

4. Orphulella speciosa
(Tested middle July to early August)

A. Tabular Synopsis of Differential Feeding Tests:

Test I.	10VF / 29VF / 28F / 134V / 1VN / 174FN & 165FN / Untouched: 2, 83, 91, 93, 96, 148, 162, 178, 179
Test II.	10V / 28F / 1V / Untouched: 91, 93, 96, 134, 165, 174, 178, 162
Test III.	10V / 28V / Untouched: 1, 134, 140, 162, 174, 178
Test IV.	29VF / 17V / 25V / 45V / Untouched: 92, 117, 135, 144, 149, 174, 179
Test V.	10VF / 16V / Untouched: 92, 96, 115, 117, 134, 149, 165, 168, 178, 181
Test VI.	10V / 27VF / Untouched: 92, 113, 115, 140, 144, 168, 178, 181
Test VII.	14V & 16V / 21V / 99VN / 98VN / Untouched: 117, 142, 144, 148, 149, 182

B. Summary of Relative Preference Value of Frequently Tested Foods:

Agropyron repens V 5:0 / Poa compressa VF 3:0 / Equisetum arvense V 1:2 / Monarda fistulosa V 1:3 / Erigeron strigosus F 0:3 & Rudbeckia serotina F 0:4

5. Pseudopomala brachyptera
(Tested early to late July)

A. Tabular Synopsis of Differential Feeding Tests:

Test I.	28VF & 10VF / 96VF / 97F / Untouched: 1, 2, 83, 125, 134, 148, 165, 174
Test II.	10VF / 28F / 96FN & 134VN / Untouched: 1, 2, 83, 148, 165, 174
Test III.	10V / 28F / 29F / Untouched: 1, 2, 70, 83, 96, 134, 148, 162, 165, 174, 178
Test IV.	10VF / 28F / 29VF / Untouched: 96, 134, 148, 162, 165, 174, 178
Test V.	10V / 28VF / 29VF / Untouched: 83, 96, 134, 148, 162, 165, 174, 178
Test VI.	10V / 29VF / 28VF / Untouched: 83, 96, 134, 148, 162, 165, 174, 178
Test VII.	10VF / 29VF / 28F / Untouched: 83, 91, 93, 96, 134, 148, 162, 165, 174, 178, 179
Test VIII.	10V / 28F / Untouched: 1, 91, 93, 96, 134, 162, 165, 174, 178
Test IX.	35V & 34V / 36V / 22V / 39V / 38VN & 45VN & 11VN / Untouched: 40
Test X.	35V & 10V / 1V & 28F & 11F / 7 VN / Untouched: 44, 45
Test XI.	35V & 10V / 28VF & 11V & 1V / 7 VN / 45VN
Test XII.	35V & 10V / 11VF & 1V / 28VN / 7VN / Untouched: 45
Test XIII.	35V & 10V / 1V / 28V / 11VN / Untouched: 7, 45

B. Summary of Relative Preference Value of Frequently Tested Foods:

Agropyron repens V 12:0 & Carex stricta var. strictior V 5:0 / Poa compressa VF 11:1 / Agrostis alba VF 3:2 & Poa pratensis VF 5:0 / Juncus tenuis V 0:5 / Melilotus alba VF 1:7 & Monarda fistulosa V 0:8

TABLE II (CONT.)
RESULTS OF DIFFERENTIAL FEEDING TESTS

6. Syrbula admirabilis
(Tested middle August to middle September)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 14V & 16V & 28VF & 10V
Test II. 28V & 10V / 1V / Untouched: 91, 111, 140, 174, 178, 179
Test III. 12VF & 16V & 29VF / Untouched: 101, 111, 144, 149, 168, 174
Test IV. 10V & 16V / 28VF / 29F / 1VN / Untouched: 91, 93, 111, 115, 117, 148, 149, 168, 178, 179
Test V. 16V & 10V / 28VF / 1V / 138VFN & 93VN / Untouched: 91, 111, 115, 117, 148, 168, 178, 179
Test VI. 13VF / 29VF / 28VF / 25VN / Untouched: 92, 93, 103, 104, 170, 172, 178, 179, 180
Test VII. 10V / 28VF / 1VN / Untouched: 2
Test VIII. 16V / 21VF & 28VF / 30F / 12F & 29F / 179VN & 117FN / Untouched: 48, 144
Test IX. 13VF / 28V / Untouched: 67, 91, 93, 104, 172, 179, 180

B. Summary of Relative Preference Value of Frequently Tested Foods:

Dactylis glomerata V 5:0 & Agropyron repens V 5:0 / Poa compressa VF 8:0 / Poa pratensis VF 4:0 / Equisetum arvense V 2:2 / Lespedeza capitata V 0:4 & Solidago nemoralis V 0:6

7. Arphia p. pseudonietana
(Tested middle August to middle September)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 10V & 29F / 28V / 1V / Untouched: 91, 93, 113, 115, 125, 140, 148, 168, 174, 178, 179, 184
Test II. 10V & 16V & 28VF / 29F / 115F & 117F / 1VN / Untouched: 91, 93, 111, 148, 149, 168, 178, 179
Test III. 28V / 16V & 10V / 1V / 117FN / 93VN / Untouched: 91, 111, 115, 138, 148, 168, 178, 179
Test IV. 28VF / 13VF / 25V / 67VN / 37VN & 179VN / Untouched: 93, 115, 140, 168
Test V. 28VF / 10V / 1V / Untouched: 2, 91, 93, 117, 134, 138, 148, 164, 176, 178, 179
Test VI. 16V / 21F / 28FN & 138FN / 117FN & 30FN / Untouched: 115, 140, 149, 168, 176
Test VII. 10V / 14V & 28VF / 138VF / 178VN / 179VN / Untouched: 1, 91, 93, 117, 148, 163, 182
Test VIII. 16V / 10V & 28F & 1V / Untouched: 91, 93, 117, 119, 148, 178, 179
Test IX. 13VF / Untouched: 28, 67, 91, 93, 104, 172, 179, 180

B. Summary of Relative Preference Value of Frequently Tested Foods:

Dactylis glomerata V 4:0 / Agropyron repens V 6:0 & Poa compressa VF 7:2 / Equisetum arvense V 4:2 / Linaria vulgaris VF 1:3 & Daucus Carota F 1:5 / Oenothera biennis F 1:4 & Solidago juncea V 0:6 & Solidago nemoralis V 0:8 & Lespedeza capitata V 0:8

TABLE II (CONT.)
RESULTS OF DIFFERENTIAL FEEDING TESTS

8. Arphia sulphurea
(Tested early June to middle July)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 29VF/ 28VF/ 134VN / 70VFN/ 183VN / Untouched: 117, 151, 170, 178, 180
Test II. 29VF / 28VF/ 134V/ 183VN/ 70FN / Untouched: 151, 170
Test III. 28VF / 29VF / 151F/ Untouched: 70, 134, 148, 162, 180
Test IV. 28VF / 180VN/ Untouched: 70, 134, 148, 162
Test V. 10V / 28VF / Untouched: 70, 83, 148, 162, 180, 184
Test VI. 10V / 28F / 165FN / Untouched: 1, 2, 70, 83, 96, 148, 184
Test VII. 27V & 16V / 25F / 29VN / 99VN / 96VN / Untouched: 70, 88, 95, 103
Test VIII. 10VF / 27VF / 29VF / 17V & 25VF / 45V / 148VF & 144F / 174F / 142F / 182V / 100V / Untouched: 81, 95, 99, 117
Test IX. 16V / 10VF / 25VF / 33V / 28VF & 45V & 17VF
Test X. 27V / 16V / 25F / 29V
Test XI. 10VF / 29VF / 25F / 17VF / 45V & 27V
Test XII. 29VF & 14V / 28F & 16V / 45V / 48V & 162F & 95V / Untouched: 113, 134, 142, 148, 165, 176
Test XIII. 16V / 14V / 29VF / 28F / 45V & 95V & 48V / 162V / Untouched: 113, 134, 142, 148, 165, 176
Test XIV. 16V / 14VF / 10V / 29FN & 28FN / 142FN & 48VN / Untouched: 134, 148, 162, 165, 176, 178
Test XV. 27VF / 17V / 29F / 45V / 144V / 89V / 98VN / Untouched: 49, 81, 99, 135, 148, 164, 176, 178
Test XVI. 27VF / 17VF / 29VF / 45V & 81V / Untouched: 49, 144, 148, 174, 176, 178
Test XVII. 100V & 99V / 70VF / 109VN & 88VN / Untouched: 103, 104, 140, 148, 176
Test XVIII. 70F / 99VN / 100VN & 95VN / Untouched: 88, 148
Test XIX. 29V / 28F / 70F / 93VN / Untouched: 178, 179, 180
Test XX. 29V / 27V / 28FN & 70VN / 134VN / Untouched: 85, 93, 178, 179, 180
Test XXI. 27VF / 29V / 28F / 70F / 85VN / Untouched: 93, 134, 162, 165, 178, 179, 180
Test XXII. 29V / 27VF / 28FN / Untouched: 85, 93, 134, 162, 165, 178, 179, 180
Test XXIII. 29V / 27V & 28F / Untouched: 85, 93, 134, 162, 165, 178, 179, 180

B. Summary of Relative Preference Value of Frequently Tested Foods:

Dactylis glomerata V 6:0 / Agropyron repens VF 6:0 / Phleum pratense VF 10:0 & Poa pratensis VF 15:2 / Panicum sp. F 5:0 / Danthonia spicata VF 5:0 & Poa compressa F 12:3 / Juncus tenuis V 7:0 / Trifolium pratense V 1:4 & Rumex Acetosella VF 4:8 & Medicago lupulina V 2:3/ Chrysanthemum Leucanthemum F 2:7/ Monarda fistulosa V 1:10 / Erigeron strigosus F 0:7 & Lespedeza capitata V 0:5 / Solidago rigida V 0:9 & Achillea Millefolium VF 1:11

TABLE II (CONT.)
RESULTS OF DIFFERENTIAL FEEDING TESTS

9. Camnula pellucida
(Tested July)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 29V / 28F / 27V / 134VN / 178VN / Untouched: 85, 93, 162, 165, 179, 180
Test II. 29V / 27VF / 28VF / 85VN / 13VN / Untouched: 93, 134, 165, 178, 179, 180
Test III. 29V / 27VF / 28F / 164VN / 13VN & 85VN Untouched: 93, 134, 165, 178, 179, 180
Test IV. 10VF / 28F & 27V / 178VN / Untouched: 93, 134, 165, 179, 180
Test V. 29V & 27VF / 28VF / 13VN / Untouched: 85, 93, 134, 165, 178, 179, 180

B. Summary of Relative Preference Value of Frequently Tested Foods:

Poa pratensis V 4:0 / Phleum pratense VF 5:0 / Poa compressa F 5:0 / Aristida purpurascens V 0:3 & Rubus flagellaris V 0:4 / Solidago juncea V 0:5 & Monarda fistulosa V 0:5

10. Chortophaga viridifasciata
(Tested middle May to middle July)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 164V / 182VF & 143V & 129V / 83VN
Test II. 164V / 182V & 143V & 129V / 99VN / 83VN
Test III. 78VF & 164V / 133V / 99V / 117VN / 129FN / 83VN / Untouched: 176
Test IV. 78VF / 99V / 164V / 133V / 129F / 117VN & 176VN / Untouched: 83
Test V. 164V / 133V & 129V / 99V / 117V / 176VN / 83VN
Test VI. 164V/ 99V / 83V / 117VN / 176VN
Test VII. 164V / 134V / 99V / 117V / 81VN
Test VIII. 164V / 117VF / 81V / 176VN
Test IX. 33V / 134V / 99V / 50VN / 176VN / 148VN
Test X. 53V / 165F / 134V / 96V / 148V / Untouched: 176
Test XI. 134V / 96VN / 162VN / 165FN / 148VN
Test XII. 48V / 134V / 162F / 176V / 95VN / Untouched: 148, 165
Test XIII. 96F / 134V / 142F / 48V / Untouched: 83, 95, 148, 162, 165, 174
Test XIV. 48V / 97VF / 96V / 134V / 174FN / Untouched: 95, 113, 117, 148, 149, 162, 165
Test XV. 48V / 142F / 96F / Untouched: 83, 95, 113, 117, 134, 148, 162, 165
Test XVI. 16VF / 14VF & 27VF / 29VF & 25VF / 33V / 28VF / 45V
Test XVII. 16VF & 14VF / 27V / 33VF / 28F / 29V / 25VF / 45V
Test XVIII. 29V & 16V & 14V / 33VF & 28VF / 25VF / 45V
Test XIX. 29VF / 16V / 14V / 28F / 45V
Test XX. 16V / 14V / 28F / 29VF & 96V & 48V / Untouched: 45, 95, 113, 134, 142, 148, 162, 165, 176
Test XXI. 16V / 14V / 29VF & 28VF / 48V & 96VF / 95V/ 142FN & 134VN & 45VN / Untouched: 113, 148, 162, 165, 176

TABLE II (CONT.)
RESULTS OF DIFFERENTIAL FEEDING TESTS

Test XXII. 14VF / 16V / 10V & 29VF / 28F / 134F & 96VF / 48V & 162F / Untouched: 148, 165, 176, 178
Test XXIII. 14VF / 16V / 29VF & 28F / 96VFN & 95VN / Untouched: 48, 104, 134, 148, 162, 165, 176, 178
Test XXIV. 27V / 16V / 14V / 134VN & 29VFN / 48VN & 28FN / 165FN & 95VN / Untouched: 96, 104, 135, 148, 162, 176, 178
Test XXV. 14VF / 78VF
Test XXVI. 29VF / 170V / Untouched: 151, 172, 178, 180
Test XXVII. 29V / 28F / 70F / Untouched: 93, 178, 179, 180
Test XXVIII. 29V / 27V / 28F / 85V / 70VFN / 178VN & 93VN / Untouched: 134, 179, 180
Test XXIX. 29V / 27V / 70VF / 28F / Untouched: 85, 93, 134, 162, 165, 178, 179, 180
Test XXX. 27V & 29V / 28F / 162V / 93VN & 85VN / 178VN / Untouched: 134, 165, 179, 180
Test XXXI. 29V / 27V / 28F / 93VN / 162VN / Untouched: 70, 85, 134, 165, 178, 179, 180

B. Summary of Relative Preference Value of Frequently Tested Foods:

Dactylis glomerata V 9:0 / Bromus inermis VF 10:0 / Phleum pratense V 7:0 & Poa pratensis VF 14:1 / Poa compressa F 13:1 / Cirsium arvense V 8:0 / Asparagus officinalis V 7:2 & Melilotus alba VF 7:3 / Juncus tenuis V 4:2 / Lespedeza capitata V 0:5 / Monarda fistulosa V 8:9 & Glechoma hederacea VF 4:1 / Medicago lupulina V 1:7 / Daucus Carota V 3:5 & Chrysanthemum Leucanthemum VF 3:10 / Erigeron strigosus F 1:13 & Solidago juncea V 0:9 / Potentilla recta V 1:7 & Solidago canadensis V 1:12 & Achillea Millefolium V 1:11

11. *Dissosteira carolina*
(Tested early August to middle September)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 10VF / 29VF & 1V / 28F / 91VN / 96VN & 149VN / Untouched: 2, 117, 125, 134, 140, 148, 157, 178, 179
Test II. 16V & 10VF / 96VF / 115F & 181F / 149VN / Untouched: 117, 134, 165, 168, 178
Test III. 10V / 27V / 144V / 181F / Untouched: 113, 115, 140, 168, 178
Test IV. 14VF & 28F & 27V & 10V / 144V & 16V & 101V / 30V / 149VN & 181FN / 178VN / Untouched: 117, 148, 168
Test V. 10V / 28F & 1V / 174F & 140V /111V / 91VN / Untouched: 157, 178, 179
Test VI. 10V / 28F & 1V / 91V / 29F / 113V & 174F / Untouched: 93, 115, 125, 140, 148, 168, 178, 179, 184
Test VII. 10V & 16V / 28VF & 1V / 29F & 111V / 117FN & 91VN & 93VN & 178FN / 168VN & 115FN & 149VN / Untouched: 148, 179
Test VIII. 28F & 10V / 16V & 19VF / 30VF & 18F & 117F & 1V / 91VN & 111VN / 93VN & 178VFN & 12FN & 138FN / Untouched: 115, 148, 168, 179
Test IX. 28VF / 25V & 37VF / 13VF / 93VN / 179VN & 140VN / Untouched: 67, 115, 168
Test X. 28V / 93VF / 172VN / Untouched: 13, 67, 91, 104, 179, 180

TABLE II (CONT.)
RESULTS OF DIFFERENTIAL FEEDING TESTS

B. Summary of Relative Preference Value of Frequently Tested Foods:

Agropyron repens V 8:0 / Poa compressa F 8:0 & Equisetum arvense V 5:0 / Desmodium illinoense V 1:5 & Daucus Carota F 1:4 & Lespedeza capitata V 1:4 & Verbascum Thapsus V 1:4 / Solidago juncea VF 0:8 & Oenothera biennis F 1:5 / Solidago nemoralis V 0:7 & Gnaphalium obtusifolium V 0:7

12. Encoptolophus s. sordidus
(Tested middle September to early October)

A. Tabular Synopsis of Differential Feeding Tests:

Test I.	33V / 16V & 17V / 12V & 28VF / 117F & 21F / 30VN / 153VN & 111VN / Untouched: 81, 113, 138, 144, 148, 159, 168, 179
Test II.	13VF / 28V / 172FN & 93VN / 67VN / Untouched: 91, 104, 179, 180
Test III.	19V / 28V & 14V / 16V / 95VN / Untouched: 119, 134, 149, 153, 159, 176
Test IV.	16V / 28V / 1V / Untouched: 93, 148, 153, 168, 176, 178, 179
Test V.	33V / 16V / 17V / 21F / Untouched: 48
Test VI.	16V / 28VF / 10VN / 1VN / Untouched: 111, 117, 138, 148, 153, 178, 179, 180
Test VII.	33V / 16V / 17V / 21VFN
Test VIII.	16V & 14V / 28VF / 12VF

B. Summary of Relative Preference Value of Frequently Tested Foods:

Carex pensylvanica V 3:0 / Dactylis glomerata V 7:0 / Danthonia spicata V 3:0 / Poa compressa VF 6:0 / Eragrostis spectabilis F 2:1 / Aster laevis V 0:4

13. Pardalophora apiculata
(Tested middle May to middle June)

A. Tabular Synopsis of Differential Feeding Tests:

Test I.	151V / 70VF / 183VN / 170VN / 172VN / Untouched: 178
Test II.	151VF / 70VF / 183VN & 172VN & 170VN / Untouched: 178
Test III.	151VF / 70VFN / 183VN & 172VN & 117VN & 134VN / Untouched: 170, 178, 180
Test IV.	134V / 117V / 183V / 70F / 151F / Untouched: 170, 172, 178, 180
Test V.	134V / 183V / Untouched: 70, 117, 170, 172, 178
Test VI.	70F / 151F / 134VN / 162FN / Untouched: 83, 148, 164, 180
Test VII.	162FN / 70FN / Untouched: 83, 134, 148, 180
Test VIII.	28V / 29V / 183V & 70F / 170V / 151VN / 178VN / Untouched: 172
Test IX.	29V / 28V / 183V / 151V / 70F / 170V / 178VN / Untouched: 172

TABLE II (CONT.)
RESULTS OF DIFFERENTIAL FEEDING TESTS

Test X. 29V / 28V / 183V / 70VF / 134V / 74V / 117VN / Untouched: 151, 170, 172, 178, 180
Test XI. 29V / 28V / 183V / 151VF / 70VF / 117V / 178VN / 134VN / Untouched: 74, 170, 172, 180
Test XII. 29V / 28V / 134V / 70V / Untouched: 117, 170, 172, 178, 180
Test XIII. 29V / 28V / 151V / 162V / 70VN / Untouched: 83, 134, 148, 180
Test XIV. 28V / 162FN / 148FN / 70FN / Untouched: 83, 134, 180
Test XV. 28V / 29V
Test XVI. 29V / 28V
Test XVII. 29V / 28V
Test XVIII. 29V / 28V
Test XIX. 29V / 28V
Test XX. 29V / 28V
Test XXI. 28VF & 151VF / 170V / Untouched: 172, 178, 180

B. Summary of Relative Preference Value of Frequently Tested Foods:

Poa pratensis V 12:0 / Poa compressa V 14:0 / Tragopogon pratensis V 6:3 & Antennaria fallax VF 9:2 / Rumex Acetosella VF 9:5 / Monarda fistulosa V 4:6 / Daucus Carota V 2:4 / Hieracium longipilum V 3:8 / Solidago juncea V 0:11 & Liatris aspera V 0:11.

14. Spharagemon b. bolli
(Tested early July to late August)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 10V / 28F & 29F & 1V / 96VF / 140VN & 91VN / Untouched: 2, 83, 113, 93, 134, 148, 162, 165, 174 178, 179
Test II. 10VF / 1V/29VF / 28F & 174F & 140V & 96VF / 134VF & 149V / Untouched: 117, 178
Test III. 10V / 92VF & 181VF / 16V / 117VF & 96VF / Untouched: 115, 134, 149, 165, 168, 178
Test IV. 10VF / 27VF / 140V / 144V/181F / Untouched: 92, 113, 115, 168, 178
Test V. 28F / 27V & 10VF & 30V & 14VF & 181VF / 16V & 101V / 144V / 178VN & 149VN / Untouched: 117, 148, 168
Test VI. 10V & 140V / 111V / 28F & 1V / 174FN & 91VN / Untouched: 178, 179
Test VII. 16V / 144V / 117F & 101V & 29F / 174F & 12F / 111VN / Untouched: 149, 168
Test VIII. 10V / 16V & 28F / 1V / 111V & 29F / 117FN & 91VN & 149VN / 115FN & 93VN / Untouched: 148, 168, 178, 179
Test IX. 1V & 138VF / 10V & 16V / 28F & 91V & 117F / 93VN & 111VN / Untouched: 115, 148, 168, 178, 179
Test X. 28F / 25V & 140V / 13VF / 93V & 37VF / 67VN / 179VN & 115VFN / Untouched: 168
Test XI. 93VF / 172VN / 104VN / Untouched: 13, 28, 67, 91, 179, 180
Test XII. 27V & 28VF / 29F / 93VN/134VN / 179VN / Untouched: 13, 85, 165, 178, 180
Test XIII. 27VF / 28F / 29V / 164VN / Untouched: 13, 85, 93, 134, 165, 178, 179, 180

TABLE II (CONT.)
RESULTS OF DIFFERENTIAL FEEDING TESTS

Test XIV. 27V / 28F / 10V / 93VN / 179VN / Untouched: 134, 165, 178, 180
Test XV. 27VF & 28VF / 178VN & 29VN & 85VN & 165VFN & 13VN / Untouched: 93, 134, 179, 180
Test XVI. 27VF / 28VF/ 134V / 93VN / 29VN / Untouched: 13, 85, 165, 178, 179, 180

B. Summary of Relative Preference Value of Frequently Tested Foods:

Phleum pratense VF 7:0 & Agropyron repens V 9:0 / Equisetum arvense V 5:0 & Dactylis glomerata V 5:0 & Poa compressa F 12:1 / Poa pratensis VF 6:2 / Verbascum Thapsus V 4:1 / Daucus Carota F 3:3 / Desmodium illinoense V 1:4 & Ambrosia artemisiifolia V 1:4 & Lespedeza capitata V 2:8 & Monarda fistulosa V 2:6/ Aristida purpurascens VF 1:5 & Oenothera biennis VF 0:5 & Solidago nemoralis V 0:11 & Erigeron strigosus VF 0:7 & Solidago juncea V 0:13

15. Spharagemon collare
(Tested middle July to early September)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 10V & 1V & 91V / 28F & 113V & 174F & 93V / 140VN / Untouched: 29, 115, 125, 148, 168, 178, 179, 184
Test II. 16V & 10V / 28F / 29F & 1V / 117F & 115F / 149VN / 93VN / 91VN / Untouched: 111, 148, 168, 178, 179
Test III. 16V / 28V / 117F & 1V & 138VF & 91V & 10V / 93V & 111V / 178FN / Untouched: 115, 148, 168, 179
Test IV. 28VF / 25V & 37VF & 93V / 13F / 115FN & 179VN & 67VN / Untouched: 140, 168
Test V. 28F & 10V & 1V / 93V & 164F & 91V / 138VFN / Untouched: 2, 117, 134, 148, 176, 178, 179
Test VI. 16V / 28F / 21VF / 138VFN & 30VFN / 117FN / Untouched: 115, 140, 149, 168, 176
Test VII. 28VF / 14V / 91V & 1V / 10V & 93V / 138VN / 117FN & 163VN / Untouched: 148, 178, 179, 182
Test VIII. 16V / 10V & 119V / 1V & 91V / 93V / 28FN / Untouched: 117, 148, 178, 179
Test IX. 28VF & 13VF / 93VF / 172VN / Untouched: 67, 91, 104, 179, 180
Test X. 27VF / 28F / 29F / 93V / Untouched: 85, 134, 162, 165, 178, 179, 180
Test XI. 27VF / 28F / 29F / 93VN / 134VN / Untouched: 13, 85, 165, 178, 179, 180
Test XII. 27VF / 28F & 29F / 164VN / 134VN / 179VN & 93VN & 13VN / Untouched: 85, 165, 178, 180
Test XIII. 27VF & 10VF / 28F / 93V / Untouched: 134, 165, 178, 179, 180
Test XIV. 27VF / 28VF / 29F / 13V / 93VN / 85VN / Untouched: 134, 165, 178, 179, 180

B. Summary of Relative Preference Value of Frequently Tested Foods:

Phleum pratense VF 5:0 & Agropyron repens V 7:0 / Poa compressa F 13:1 / Equisetum arvense V 6:0 / Poa pratensis F 5:1 & Desmodium illinoense V 5:2 / Lespedeza capitata V 9:4 / Daucus Carota F 2:4 / Monarda fistulosa V 0:6 / Oenothera biennis F 1:4 / Solidago juncea F 0:11 & Solidago nemoralis V 0:13

TABLE II (CONT.)
RESULTS OF DIFFERENTIAL FEEDING TESTS

16. Melanoplus b. bilituratus
(Tested early July to middle August)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 28VF & 10V / 97VF / 134V & 96VF / 162FN / 165FN / Untouched: 1, 2, 83, 125, 148, 174
Test II. 10V / 28VF / 134V / 96VF / 1V / 174F / 2F & 165F & 83F & 148VF & 162F / 70VN
Test III. 10V / 29F / 178V & 28F / 96VF / 174F & 162F / 134V / 165F & 83F & 148V / Untouched: 1, 2, 70
Test IV. 10VF / 28F & 29VF / 96VF & 174VF & 134V / 178V & 165F & 148V / Untouched: 70, 162
Test V. 10VF / 29VF / 96VF & 28F / 178V / 174F / 165FN & 134VN / 148VF / Untouched: 83, 162
Test VI. 10V / 162F / 29VF / 28VF & 96VF & 174F & 178V / 134VF / Untouched: 83, 91, 93, 148, 165, 179
Test VII. 10VF / 29VF & 178V / 96VF / 28F & 134VF / 174F & 83F & 165F & 162F / Untouched: 91, 93, 148, 179
Test VIII. 10V / 28F & 162F & 178V / 165F & 174VF / 1V / 134VFN & 96VFN / Untouched: 29, 83, 91, 93, 148
Test IX. 10V / 1V / 178V / 28F & 174F & 134F & 162V / 29V / 140VN
Test X. 10V / 1V / 29VF / 96VF & 178VF & 134F & 174VF / 28FN & 140VN & 149VN / Untouched: 117
Test XI. 10V / 96VF / 16V / 134VF & 181F / 92VFN & 149VN & 165FN & 178VFN / 115VN & 168VN / 117FN
Test XII. 14VF / 16V / 28VF
Test XIII. 179F / 180F / 93V / 172FN / 91VN / Untouched: 13, 28, 67, 104
Test XIV. 29V / 27VF / 28VF / 134V & 165F / 178VN / 85VN / Untouched: 13, 93, 179, 180
Test XV. 27VF / 29V / 28F / 85VN & 134VN & 164VN / Untouched: 13, 93, 178, 179, 180
Test XVI. 27V / 10V / 28F / 178VN & 165VFN / Untouched: 93, 134, 164, 179, 180
Test XVII. 27VF & 29V / 28VF / 134V / 85VN & 179VN & 178VFN & 165FN / Untouched: 13, 93, 180
Test XVIII. 27VF / 29V / 134VF / 28F & 178V / 85VN & 165VFN / 93VN / Untouched: 13, 179, 180

B. Summary of Relative Preference Value of Frequently Tested Foods:

Phleum pratense VF 5:0 & Agropyron repens V 12:0 / Poa pratensis VF 11:1 / Poa compressa F 15:2 / Melilotus alba VF 9:1 / Solidago juncea V 9:5 / Rudbeckia serotina F 9:1 & Monarda fistulosa VF 12:4 & Chrysanthemum Leucanthemum F 6:3 / Erigeron strigosus F 6:7 / Achillea Millefolium VF 4:4 & Potentilla recta F 3:4 / Solidago nemoralis VF 1:7 & Solidago rigida F 1:5 & Lespedeza capitata V 1:8

17. Melanoplus bivittatus
(Tested early August to middle September)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 9V & 7V / 27V & 34V & 39V / 41F / 130VN & 166VN & 36VN / 72VN & 22VN & 38VN / Untouched: 11, 45, 46, 106, 122, 124, 132, 139, 154
Test II. 9V / 44V / 38V / 7V & 167V / 11F & 36V / 139VFN & 130VN & 22VN & 39VN / Untouched: 45, 46, 72, 154
Test III. 9VF / 56V & 11F / 39V / 166V / 126VF / 36VN / Untouched: 34, 46, 124, 139, 167, 181

TABLE II (CONT.)
RESULTS OF DIFFERENTIAL FEEDING TESTS

Test IV.	9V / 7V / 11F & 56V & 130V & 55V / 36VFN & 39VN / 167VN & 34VN / 72VN / Untouched: 46, 106
Test V.	7V & 9V / 11F / 38VF & 167F & 166VF & 55V / 72V & 39VF & 46F / 176VFN & 41FN & 34VN & 36VN
Test VI.	9V / 7V / 41F & 166VF / 22V & 117F & 167VF & 55V / 34VN & 11FN / 36VN & 46VFN & 39VN
Test VII.	108V & 7V / 116F & 87F & 136V / 167VF / 109V / 15VF / 56VN & 160VFN / 3VN & 59VN / 82VN & 35VN
Test VIII.	9V / 117F & 7V / 167VF & 166VF / 39V & 176V & 36V & 181F / 11FN / Untouched: 22, 33, 41, 46
Test IX.	9V / 181F / 117FN & 41FN & 22FN / 7VN & 39VN & 72VN & 176FN & 166FN & 56VN / Untouched: 36, 46, 122, 167
Test X.	108V / 82F / 7V & 35V / 109VN & 87VN / 159VN / Untouched: 15, 59, 160

B. Summary of Relative Preference Value of Frequently Tested Foods:

Sagittaria latifolia V 8:0 / Typha latifolia V 8:1 / Eupatorium perfoliatum VF 4:2 / Eupatorium purpureum VF 5:3 & Agrostis alba F 4:3 / Scirpus atrovirens V 4:4 / Carex vulpinoidea V 2:6 & Carex retrorsa V 1:4 & Tovara virginiana V 1:4 / Juncus Torreyi VF 1:7

18. Melanoplus confusus
(Tested early July to early August)

A. Tabular Synopsis of Differential Feeding Tests:

Test I.	10VF / 28VF / 97VF & 96VF / 162F / 165F / 148V & 174F & 125V & 2F / 134VN & 1VN / Untouched: 83
Test II.	28VF & 10VF / 165VF & 162VF & 1V & 96VF & 70VF / 134V & 148VF & 83F & 174VF / Untouched: 2
Test III.	10VF / 29F / 28F & 70VF & 165F & 162F / 174VF & 178V / 96VF & 1V & 134V / 2FN & 83FN & 148FN
Test IV.	10VF / 28VF & 178V & 29VF & 162VF / 174F / 96VF & 165F / 148VF / Untouched: 134
Test V.	10V / 162VF / 29VF & 178V / 96VF & 174VF / 165F & 134V & 28VF / 148V
Test VI.	10VF / 29VF & 162VF & 174VF / 96VF & 178V / 134VF / 165F & 28VF / 148V / Untouched: 83, 93, 179
Test VII.	10VF & 29VF / 162F & 178V / 28F & 174F / 96VF & 134F / 165F / Untouched: 83, 91, 93, 148, 179
Test VIII.	10VF & 162F & 178V / 174F / 28F & 96VF & 1V / 165F / 134FN & 93VN / Untouched: 91
Test IX.	10VF & 178V / 1V & 174F & 162VF / 28VF & 134 F / 29V / Untouched: 140
Test X.	10VF / 178VF / 174F & 1V & 117F /134V & 149V & 96VF / 28FN & 29FN / Untouched: 140
Test XI.	10V & 181VF / 115F & 92VF & 117F & 96VF / 134VF / 16VN & 149VN & 165FN / Untouched: 168, 178
Test XII.	16V / 28FN & 14VN
Test XIII.	1V & 48V / 96VF / 174VF / 178V / 162F & 165F / 134V / 83FN / Untouched: 2, 70, 148
Test XIV.	162F / 174F / 134V & 178V / 165F & 96VF / 1V & 83F / 148FN / Untouched: 2, 70
Test XV.	29VF / 16V / 14V / 27V / 25F / 45VF / 17VF
Test XVI.	28F / 70F & 178V / 179V & 180V / 29VN / Untouched: 93
Test XVII.	27V / 28VF / 134V / 70V / 85V / 93VN & 178VN / 29VN & 179VN / Untouched: 180

TABLE II (CONT.)
RESULTS OF DIFFERENTIAL FEEDING TESTS

Test XVIII. 27VF / 162F & 70VF / 178V & 134V / 165V / 28F / 179VN & 29VN / Untouched: 85, 93, 180
Test XIX. 27VF / 162VF / 178V & 134V / 85V / 165VFN / 28VN / 29VN / Untouched: 93, 179, 180
Test XX. 27VF / 162F & 134VF / 178V / 179V & 165VF / 93VN & 28VN & 29VN & 85VN / Untouched: 180
Test XXI. 27VF / 178V / 165F / 134V & 28VF / 179VN / Untouched: 13, 85, 93, 180
Test XXII. 27VF / 164V / 134VF & 165F / 178VN & 29VN & 85VN / Untouched: 13, 28, 93, 179, 180

B. Summary of Relative Preference Value of Frequently Tested Foods:

Agropyron repens VF 11:0 & Phleum pratense VF 7:0 / Chrysanthemum Leucanthemum F 14:0 / Solidago juncea V 15:3 / Rudbeckia serotina F 12:0 / Poa compressa VF 13:5 & Melilotus alba VF 12:0 & Erigeron strigosus F 14:2 & Equisetum arvense V 7:1 & Monarda fistulosa VF 16:3 / Achillea Millefolium VF 5:4 / Potentilla recta F 2:5 & Rubus flagellaris V 2: 4 & Solidago nemoralis V 2:7 / Equisetum hyemale F 1:4 & Lespedeza capitata V 0:10 & Solidago rigida V 1:6

19. Melanoplus f.-r. femur-rubrum
(Tested early September to early October)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 10V & 182VF & 117VF / 14V / 178V & 138VF & 111V & 174F / 134V / 28F & 164F & 163F / 1VN / 91VN & 179FN / Untouched: 2, 93, 115, 148, 168, 184
Test II. 117VF / 16V & 10V & 179VF / 119V / 178V / 91VN & 93VN / Untouched: 1, 28, 148
Test III. 179F / 180VF / 172VF / 91V / 13FN & 104VN / Untouched: 28, 67, 93
Test IV. 159F & 16V / 153F / 19VF & 14V / 95V & 134V / 176VFN / Untouched: 28, 119, 149
Test V. 153F / 176VF & 16V & 6V / 178V / 148VN / 93VN / Untouched: 1, 28, 168, 179
Test VI. 117V / 175VF & 153VF / 159F & 16V / 138F & 109V / 144VFN & 48VN / 17VN / 81VN & 21FN & 33VN / Untouched: 94, 114, 148
Test VII. 7V / 167V / 72V & 130V & 154VF / 156VF / 39VN / 46VN & 38VFN & 22VN / Untouched: 34, 41
Test VIII. 175VF & 16V / 159F & 99V / 153F & 156F / 138F / 144VN / Untouched: 17, 33, 81, 86, 148, 178

B. Summary of Relative Preference Value of Frequently Tested Foods:

Aster laevis F 4:0 & Dactylis glomerata V 5:0 / Solidago juncea V 3:1 / Solidago nemoralis F 2:2 / Lespedeza capitata V 0:4 & Achillea Millefolium V 0:5 & Poa compressa F 1:4

TABLE II (CONT.)
RESULTS OF DIFFERENTIAL FEEDING TESTS

20. Melanoplus keeleri luridus
(Tested late August to middle September)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 117VF / 1V / 16V & 178VF / 10V / 91V & 115F & 179F / 138VF / Untouched: 28, 93, 111, 148, 168
Test II. 180F & 170VF & 172F & 178VF / 28FN & 179VFN & 92VFN / Untouched: 13, 25, 93, 103, 104
Test III. 10V & 138VF / 1V & 117VF / 178VF & 134V / 164F / 176VFN / 179VFN & 91VN / Untouched: 2, 28, 93, 148
Test IV. 159F & 117F / 144VF & 142VF / 21F & 30F / 16V / 138F & 99VF / 179VFN & 149FN / 28FN / Untouched: 12, 48, 93
Test V. 182VF / 117F & 10V & 14V / 178V & 138VF / 91VN & 179FN / Untouched: 1, 28, 93, 148, 163
Test VI. 178V & 10V / 179F & 117F / 119VN / 16VN / Untouched: 1, 28, 91, 93, 148
Test VII. 172F / 179F / 180F / Untouched: 13, 28, 67, 91, 93, 104
Test VIII. 153F / 159F / 134V / 16V & 95V / 149VFN & 14VN / 19FN / Untouched: 28, 119, 176

B. Summary of Relative Preference Value of Frequently Tested Foods:

Daucus Carota F 5:0 / Solidago juncea VF 5:0 / Solidago nemoralis F 3:4 / Desmodium illinoense V 1:4 / Poa compressa F 0:8

21. Melanoplus s. scudderi
(Tested late August to late September)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 99VF / 117F & 16V / 138VF & 159F / 142VF & 144VF / 28FN & 149VFN / 179FN & 12FN / Untouched: 21, 30, 48, 93
Test II. 117VF & 182VF & 10V / 178V / 138VF / 93V & 14V & 1V / 91VN & 28FN & 163FN / Untouched: 148, 179
Test III. 10V / 179VF & 16V / 178V & 117F & 119V / 93VN / 1VN / 91VN / Untouched: 28, 148
Test IV. 179F / 172F / 93V / 180F / 104VN / Untouched: 13, 28, 67, 91
Test V. 153F / 159F / 16V / 19V & 95V / 134V / 14VN / 149VFN & 176VFN / Untouched: 28, 119
Test VI. 153F / 16V / 176VF / 179VF & 178V & 148V / 93VN / Untouched: 1, 28, 168
Test VII. 175VF / 153F / 159F & 148V / 109VN & 138VFN & 144VN / 16VN & 17VN / Untouched: 21, 33, 48, 81, 94, 114, 117
Test VIII. 153VF / 10V / 138VF & 117F / 148VN / 178VN & 179FN / Untouched: 1, 28, 111, 180
Test IX. 176F / 99VF & 182V / 14V / 117VF / 16VN
Test X. 176VF / 182V / 14V / 117VF & 99VF / 16V

TABLE II (CONT.)
RESULTS OF DIFFERENTIAL FEEDING TESTS

B. Summary of Relative Preference Value of Frequently Tested Foods:

Aster laevis F 4:0 / Solidago canadensis VF 3:1 & Daucus Carota VF 6:1 / Dactylis glomerata V 5:2 & Linaria vulgaris VF 3:1 & Solidago juncea V 3:1 / Solidago nemoralis F 3:3 / Lespedeza capitata V 2:3 & Achillea Millefolium V 2:3 & Equisetum arvense V 1:3 / Poa compressa F 0:7

22. Paroxya hoosieri
(Tested middle August to middle September)

A. Tabular Synopsis of Differential Feeding Tests:

Test I.	9V / 7V & 119V & 166V & 167VF & 11F / 38VF & 130VF / 126VN & 56VN & 139VFN / 39FN & 154VN / 36VN / Untouched: 22, 34, 46, 55, 72, 106, 122
Test II.	9V / 7V / 166VF & 167VF / 34V & 36V / 72VN & 176VN & 41VN / Untouched: 11, 38, 39, 46, 55
Test III.	9V / 166VF & 7V / 117F / 167VF / 22FN / Untouched: 11, 34, 39, 41, 46, 55
Test IV.	108V & 116F / 109V & 136V / 7V / 15VF & 82VF & 87F & 160VF / 59V & 167F / 56VN / 35VN / Untouched: 3
Test V.	9V / 7V & 117VF / 36V & 166VF & 167VF / 176V & 38V & 181F / 41FN & 22FN / Untouched: 11, 46
Test VI.	9V / 117F & 169F & 181F / 166V & 176F & 7V / 36VN / 46VN / Untouched: 22, 39, 41, 56, 72, 122, 167
Test VII.	160VF & 9V & 43V / 108VF / 166VF / 176VF / 7V & 131VF / 126VN & 32VN & 39VN/ Untouched: 44
Test VIII.	9V / 130VF / 181F / 176VF & 154VF & 177VF / 7VN & 117FN / 39VN / Untouched: 46, 54, 56, 72
Test IX.	160VF & 108V / 109V & 7V / 159FN / 15VN & 87VFN / Untouched: 35, 59, 82

B. Summary of Relative Preference Value of Frequently Tested Foods:

Sagittaria latifolia V 7:0 / Typha latifolia V 8:1 & Eupatorium perfoliatum VF 6:0 / Eupatorium purpureum VF 5:1 & Solidago canadensis VF 4:1 / Scirpus atrovirens VF 0:6 & Juncus Torreyi V 0:6

23. Schistocerca lineata
(Tested middle August to middle September)

A. Tabular Synopsis of Differential Feeding Tests:

Test I.	93V / 10V & 91V / 1V & 174V / 184VN & 28FN / Untouched: 29, 37, 113, 115, 125, 140, 148, 157, 168, 178, 179
Test II.	93V / 16V / 10V / 1V & 29F / 115VFN & 28FN / 117FN & 91VN & 111VN & 178FN / Untouched: 148, 149, 168, 179
Test III.	93V / 111V & 91V & 10V & 16V / 1V / 28F / 179VN & 115VN / Untouched: 117, 138, 148, 168, 178
Test IV.	103VF & 93VF & 104V / 92VF / 28F & 178F / 29FN / 13FN & 180VN & 179VN / Untouched: 25, 170, 172
Test V.	93VF / 91V / 10V & 1V / 138VF & 28VF / 176FN & 179VN / Untouched: 1, 2, 117, 134, 148, 178
Test VI.	16V / 140V / 30F / 149VFN / 138VN / Untouched: 21, 28, 115, 117, 168, 176
Test VII.	93VF / 163F / 14V / 138VF / 91VN & 1VN / 28FN & 10VN & 117FN / Untouched: 148, 178, 179, 182

TABLE II (CONT.)
RESULTS OF DIFFERENTIAL FEEDING TESTS

Test VIII. 93VF / 119V / 16VN & 10VN / 91VN / Untouched: 1, 28, 117, 148, 178, 179
Test IX. 93VF / 67V & 104V / 91VN / Untouched: 13, 28, 172, 179, 180
Test X. 85V / 63V / 94VF & 93V & 30V & 104V & 103F / 179VN / Untouched: 13, 28, 134

B. Summary of Relative Preference Value of Frequently Tested Foods:

Lespedeza capitata VF 9:0 / Dactylis glomerata V 3:1 / Agropyron repens V 4:2 & Desmodium illinoense V 3:4 / Equisetum arvense V 4:2 / Linaria vulgaris VF 2:2 & Poa compressa F 3:7 / Oenothera biennis VF 0:4 / Daucus Carota F 0:6 & Solidago nemoralis V 0:9 & Solidago juncea F 1:6

24. Amblycorypha oblongifolia
(Tested middle August to middle September)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 178F & 169F / 134F & 141VF & 117F / 101VF & 111V & 113V & 119V & 110V & 109V / 146VN / Untouched: 14, 16, 36, 47, 174, 175
Test II. 119V / 178F & 109V & 115F & 101VF & 117VF / 111VN & 149VN / 110VN / Untouched: 14, 30, 50, 138, 144, 174, 176
Test III. 108VF & 176VF / 128V & 169F / 175VF & 109V / 135VF & 90V / 119VN / Untouched: 4, 20, 110, 155
Test IV. 176VF / 169F & 101V & 135VF & 128V / 109V & 119V / 90VN / 121VFN / Untouched: 145, 155
Test V. 176VF & 108V & 116F / 169F & 109V / 75V / 61VN / Untouched: 52, 110
Test VI. 117F & 72V & 9V & 7V & 181VF / 41F & 167VF & 56V / 22FN & 166FN & 122VN / 39FN & 38FN / Untouched: 11, 36, 46, 55, 106
Test VII. 176F / 9V / 117F / 169F & 181F / 167VF / 72VN & 41FN & 7VN & 166FN / Untouched: 22, 36, 39, 46, 56, 122
Test VIII. 108VF / 176VF & 9V / 131V & 32V / 7V / 166VN & 126VN / Untouched: 39, 43, 44
Test IX. 179F / 111V / 152F / 84VN / 67VN

B. Summary of Relative Preference Value of Frequently Tested Foods:

Impatiens capensis VF 3:0 / Solidago canadensis VF 5:1 / Sagittaria latifolia V 3:0 / Daucus Carota F 4:0 & Helianthus divaricatus F 5:0 / Oxalis stricta VF 3:0 & Cornus stolonifera V 3:1 & Rhamnus alnifolia V 5:0 / Vitis riparia V 2:1 & Typha latifolia V 2:1 / Parthenocissus quinquefolia V 1:3 / Eupatorium perfoliatum VF 0:3 / Scirpus atrovirens F 0:3

TABLE II (CONT.)
RESULTS OF DIFFERENTIAL FEEDING TESTS

25. Amblycorypha rotundifolia
(Tested middle August to middle September)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 178F & 169F / 134F & 111V & 101VF & 141F & 117F / 174F & 113VF / 110V & 119V & 109V / 175VF / 146F / Untouched: 14, 16, 36, 47
Test II. 115F / 111V & 101VF & 109V & 110V & 178F / 176V & 117VF & 138F & 30V / 174FN & 119VN / Untouched: 14, 50, 144, 149
Test III. 108VF / 135VF & 128V & 169VF / 175VF & 176VF / 119V & 109VF / 119V & 109V / 90VN & 110VN / Untouched: 4, 20, 155
Test IV. 135F & 169VF & 101V / 128V & 119V & 109V / 176VF / 121VN / Untouched: 90, 145, 155
Test V. 108V / 169F / 75V & 110V & 116VF / 109VN & 176VN / Untouched: 52, 61
Test VI. 176VF / 147F & 169F / 113VF & 120V & 137F / 119V & 117F / 149VN / 179VN / Untouched: 12, 28, 64, 84
Test VII. 108VF / 169F & 176VF / 110V & 152F / 150F / Untouched: 79, 109, 161
Test VIII. 176VF / 110V / 111V & 84V / 51VN & 47VN / 119VN / Untouched: 74
Test IX. 179F / 111VN / 67VN / 84VN / Untouched: 159

B. Summary of Relative Preference Value of Frequently Tested Foods:

Impatiens capensis VF 3:0 / Helianthus divaricatus F 6:0 / Oxalis stricta VF 3:0 & Solidago canadensis VF 6:1 / Vitis riparia V 3:1 & Parthenocissus quinquefolia V 5:1 & Daucus Carota F 3:0 / Rhamnus alnifolia V 4:2 / Cornus stolonifera V 4:2 / Prunus serotina V 1:2

26. Scudderia c. curvicauda
(Tested middle August to middle September)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 7V / 9V / 119V & 106V / 11F & 72V & 56V & 55V / 126F / 167FN & 36VN & 139VFN / 38FN & 34VN / Untouched: 22, 39, 46, 122, 130, 156, 166
Test II. 7V / 9V / 38V & 72V & 11F / 55V & 166VF / 176VN & 46VN & 36VN / Untouched: 34, 39, 41, 167
Test III. 7V & 9V / 117VF / 167VF & 11F / 55VN & 166FN / Untouched: 22, 34, 41, 46, 39
Test IV. 108VF / 116F / 136V & 109V / 82VF & 167F & 59V / 87F & 160V / 15VFN / 7VN/56VN / Untouched: 3, 35
Test V. 181F / 9V / 117F / 176VN & 41FN & 7VN / Untouched: 11, 22, 36, 38, 39, 46, 166, 167
Test VI. 108VF / 176F & 150F / 169F / 161FN & 109VN / 152FN / Untouched: 79, 110
Test VII. 108VF / 43V / 176F & 131VF / 160FN & 32VN / Untouched: 7, 9, 39, 44, 126, 166
Test VIII. 181F / 177F / 117F & 156VF / 130FN & 72VN / Untouched: 7, 9, 39, 46, 54, 56, 176
Test IX. 160F / 108V / 159F / 109VN & 59VN / 35VN / Untouched: 7, 15, 87
Test X. 9V / 117VF & 7V / 160F & 69VF / 108F / 176FN

TABLE II (CONT.)
RESULTS OF DIFFERENTIAL FEEDING TESTS

B. Summary of Relative Preference Value of Frequently Tested Foods:

Sagittaria latifolia V 5:2 & Daucus Carota VF 4:0 & Impatiens capensis VF 5:0 / Typha latifolia V 4:5 / Solidago canadensis VF 2:4 & Agrostis alba F 3:1 / Eupatorium purpureum F 2:3 & Eupatorium perfoliatum VF 1:4 / Juncus Torreyi V 0:5

27. Scudderia septentrionalis
(Tested middle July)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 174F / 111VN & 176VN / 110VN & 109VN & 165FN / Untouched: 31, 50, 63, 79, 84, 86, 122, 134, 159, 175
Test II. 4V / 107V / 77VN / 174FN & 84VN / Untouched: 28, 31, 57, 63, 86, 90, 134, 159

28. Neoconocephalus ensiger
(Tested early August to early September)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 27VF / 17F & 16F / 29F / Untouched: 49, 98, 103, 117, 135, 144, 148, 149, 165, 174
Test II. 12VF / 30F / 28F / 16F & 14F / Untouched: 98, 99, 101, 103, 117, 142, 144, 148, 149, 182, 183
Test III. 12F / 30F & 19F / 28F & 14F / 16FN
Test IV. 12F & 29F / 28F / Untouched: 1, 7
Test V. 12F / 18F / 29F & 28F & 19F / 30FN & 20FN
Test VI. 12F / 29F / 28FN / 20FN
Test VII. 11F / 22F/ 38F / 41FN & 39FN & 29FN / Untouched: 7, 34, 36, 46, 166, 167
Test VIII. 11F / 39F / 41F & 38F / 22F / 167FN / Untouched: 7, 9, 36, 46, 117, 166, 176, 181
Test IX. 21F & 12F / 30F / 29F & 28F / Untouched: 48, 117, 144, 179
Test X. 26F / 15F / Untouched: 7, 35, 59, 82, 87, 108, 109, 159, 160
Test XI. 30F / 111F (fruit) / 18F / 86FN (fruit) / Untouched: 80, 146

B. Summary of Relative Preference Value of Frequently Tested Foods:

Andropogon Gerardi F 6:0 / Setaria glauca F 4:1 & Poa pratensis F 5:1 / Poa compressa F 5:1

29. Conocephalus f. fasciatus
(Tested early August to middle September)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 11F / 41F / 27V / 130V & 22V / 154V & 38F / Untouched: 7, 9, 34, 36, 39, 45, 46, 72, 106, 122, 124, 132, 139, 166

TABLE II (CONT.)
RESULTS OF DIFFERENTIAL FEEDING TESTS

Test II. 9V / 11F / 39F / 44VN & 38VFN / 22VN / Untouched: 7, 36, 45, 46, 72, 130, 139, 154, 167
Test III. 11F / 9VF & 181F / 139FN / 56VN & 36FN / Untouched: 34, 39, 46, 124, 126, 166, 167
Test IV. 11F / 124F & 46F / 167VN & 41FN / Untouched: 9, 39, 55, 56, 166
Test V. 11F / 9V & 41F / 38V & 167F / 166F / 7VN / 46VFN / 34VN & 39FN / Untouched: 36, 176
Test VI. 22F & 11F / 9V / 39F & 41F & 46F & 117F & 166VF / 7VN & 34VN & 167VN / Untouched: 55
Test VII. 22F / 166VF & 11F / 9V/38FN & 39FN & 167FN & 41FN / Untouched: 7, 34, 36, 46
Test VIII. 22F / 11F / 166F & 181F / 38VN & 41FN & 167FN & 117FN & 39FN / 9VN / 46VN & 7VN / Untouched: 36, 176
Test IX. 28F / 30F / 21F / 144VN & 117FN & 138FN / 142FN & 99FN & 93VN / Untouched: 12, 16, 48, 149, 179
Test X. 26F / 15F / Untouched: 7, 35, 59, 82, 87, 108, 109, 159, 160

B. Summary of Relative Preference Value of Frequently Tested Foods:

Agrostis alba F 8:0 & Leersia oryzoides VF 4:1 / Scirpus validus F 3:3 & Sagittaria latifolia V 5:3 & Eupatorium perfoliatum VF 4:3 / Eleocharis calva VF 2:3 / Scirpus atrovirens F 2:6 & Eupatorium purpureum VF 1:6 & Juncus Torreyi VF 2:5 / Typha latifolia V 0:7 & Carex retrorsa V 0:5 & Carex vulpinoidea F 0:6

30. Orchelimum gladiator
(Tested middle July to middle August)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 11F / 9V / 38F & 46V / 166FN & 130VN & 22VN / Untouched: 7, 34, 36, 39, 41, 56, 98, 106, 122, 124, 154
Test II. 9V & 10F & 38F & 11F / 39VN & 121VN / 132FN / 130VN & 46FN / Untouched: 7, 34, 36, 41, 45, 96, 98, 116, 124, 154
Test III. 9V & 11F / 38F / 39VN & 121VN / 132VN & 98VN & 96FN & 34VN / Untouched: 1, 7, 27, 36, 45, 46, 72, 126
Test IV. 9V & 11F / 154V & 139F & 130V / 34VN & 1VN / 38FN & 46VN / 22VN / Untouched: 36, 39, 45, 71, 124
Test V. 9VF / 8V & 11F / 181F & 36V & 139F / 154VN & 38FN / Untouched: 34, 39, 45, 46, 166
Test VI. 11F / 41F / 38F / 9VN & 181FN / 132VN / Untouched: 36, 39, 46, 45, 117, 126, 130, 139
Test VII. 9V / 72V & 11F / 38VFN & 44FN & 167VN / Untouched: 7, 22, 36, 39, 45, 46, 130, 139, 154
Test VIII. 9V / 11F / 124F / 166F & 167F / 56VN & 39FN / Untouched: 41, 46, 55
Test IX. 11F / 41F / 166VF & 9V & 167F / 38FN / 176VN & 34VN / Untouched: 7, 36, 39, 46
Test X. 9V / 41F & 11F / 22F / 117F & 166F / Untouched: 7, 34, 36, 39, 46, 55, 167

B. Summary of Relative Preference Value of Frequently Tested Foods:

Sagittaria latifolia V 9:1 & Agrostis alba F 10:0 / Eleocharis calva F 4:4 / Lycopus americanus V 1:4 / Aster lateriflorus V 1:4 / Carex retrorsa V 0:7 & Scirpus atrovirens VF 0:10 & Carex vulpinoidea V 1:8

TABLE II (CONT.)
RESULTS OF DIFFERENTIAL FEEDING TESTS

31. Orchelimum nigripes
(Tested late September)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 22F / 9V / 42F & 32F / 7FN / Untouched: 56, 119
Test II. 22F / 9F / 32VN / Untouched: 7, 42, 56, 119

32. Oecanthus nigricornis quadripunctatus
(Tested middle September to middle October)

A. Tabular Synopsis of Differential Feeding Tests:

Test I. 179F / 176F / 138F / Untouched: 1, 10, 28, 84, 86, 93, 102, 111, 134, 168, 178
Test II. 179F / 153F / 176F / 157FN / Untouched: 1, 16, 28, 93, 148, 168, 178
Test III. 153F / 138F / 159F & 175F / Untouched: 16, 17, 21, 33, 48, 81, 94, 109, 114, 117, 144, 148
Test IV. 153F / 138F & 157F / 117F & 179F / Untouched: 1, 10, 28, 111, 148, 178, 180
Test V. 175F / 153F / 138F / 159FN / Untouched: 156, 174
Test VI. 157F / 138F & 156F & 154F / Untouched: 117, 153, 164
Test VII. 156F / 99F / 153F & 159F / 117F & 148F
Test VIII. 156F / 154FN / 176FN

B. Summary of Relative Preference Value of Frequently Tested Foods:

Aster novae-anglieae F 3:1 / Aster laevis F 5:1 / Linaria vulgaris F 5:0 / Daucus Carota F 2:2 / Achillea Millefolium F 1:3

[18] Formulation and use of data obtained during the differential feeding tests:

The data obtained from the differential feeding tests are presented individually in Table II, which includes, for each species of Orthoptera, a Tabular Synopsis of Differential Feeding Tests and a Summary of Relative Preference Value of Frequently Tested Foods.

The Tabular Synopsis of Differential Feeding Tests, Table IIA, shows the relative amount of feeding by individuals of a species of Orthoptera on different food-plants during each of several tests. The foods are arranged in categories of decreasing acceptance separated from one another by the symbol /. Two or more plants in the same category have equal preference ratings. Certain letters (V, F, N) are listed with the code numbers representative of the food-plants. The symbol V denotes eating of vegetative parts of a plant, including leaves and stems; F that of floral or reproductive parts, including flowers and fruits; and N denotes nibbling, which is here defined as feeding for a period so short as to result in negligible

TABLE II (CONT.)
RESULTS OF DIFFERENTIAL FEEDING TESTS

damage to the food. Where nibbling is not specified, eating is implied. The seasonal period during which testing occurred appears under each feeder's name; this latter is important in disclosing the seasonal condition of the food-plants at the time of feeding. The reader will note that code numbers have been substituted for the names of plant species. While it would be desirable to write out the name of each plant every time it is used, it has been necessary to make this compromise between clarity and economy; thus, the identity of the food-plants must be obtained by reference to Appendix C, Plants Used in Study.

The Summary of Relative Preference Value of Frequently Tested Foods, Table IIB, shows the relative preference value of each species of food-plant tested often enough to give dependable results, and it also includes notations concerning the food parts usually selected. Its formulation is fairly simple. The Tabular Synopsis of a given species of Orthoptera is first examined to discover the identity of all frequently tested plants; such plants are usually those tested five or more times. The relative preference value of each food is then determined graphically.

Let us suppose that there are the following preferences in three tests: Test I. 9 / 3 / 15 & 8; Test II. 9 / 3 / 15 / 8; Test III. 9 / 15 / 3 / 8. Each time a food-plant is preferred over another it receives a point; each time plants are equally preferred, each receives a point. If plant 9 (Sagittaria latifolia, as shown by examination of Appendix C) is plotted in this manner against the other three plants, the result of Test I is as shown in Text Fig. 1, below:

Fig. 1

Preferred \ Not Preferred	3	8	9	15
3				
8				
9	1	1		1
15				

Fig. 2

Preferred \ Not Preferred	3	8	9	15
3				
8				
9	111	111		111
15				

Fig. 3

Preferred \ Not Preferred	3	8	9	15
3		111		11
8				1
9	111	111		111
15	1	111		

Fig. 4

Preferred \ Not Preferred	9	3	15	8
9		3	3	3
3			2	3
15		1		3
8			1	

TABLE II (CONT.)
RESULTS OF DIFFERENTIAL FEEDING TESTS

If plant 9 is plotted against the other three plants in all three tests, the graph will appear as in Text Fig. 2, above. When all four plants have been plotted against one another in the three tests, the graph will appear as in Text Fig. 3, above. By comparison of numbers, the preferred plants may then be selected and shaded to make them stand out on the graph. After a rearrangement of the plants in order of preference, the graph will appear as in Text Fig. 4, above.

It is apparent, on examination of Text Fig. 4, that 9 / 3 / 15 / 8, which is the basic information found in the Summary of Relative Preference Value of Frequently Tested Foods. The above graphs used in the formulation of the Summary are not essential to its presentation and, therefore, have been omitted.

The Summary of Relative Preference Value of Frequently Tested Foods also includes notations concerning parts of plants selected for feeding, whether vegetative or floral, and the acceptance-rejection ratio. The latter, which is a comparison of the frequency of eating as opposed to that of nibbling and complete rejection, usually shows a high degree of correlation with the preference values of food-plants; as preference decreases, rejections and nibbling tend to increase, and vice versa. In general, it was found that, whenever the acceptance-rejection ratio is 2:1 or greater, the food is relatively attractive to the feeder; whenever the ratio is 1:1 or less, the food is relatively unattractive.

Because of this close correlation the acceptance-rejection ratio may often be used in estimating the relative attractiveness of foods. Plants equally acceptable on the basis of scattered feeding experiments often can be ranked more accurately using the ratio. For example, a plant having an acceptance-rejection ratio of 13:5, but tied with one having a ratio of 2:7, is probably preferred. The former ratio indicates consistent and the latter inconsistent acceptance.

Plants not listed in the Summary of Relative Preference Value of Frequently Tested Foods because they were insufficiently tested can also be ranked, though grossly, if they have been tested one or more times. This is accomplished by comparison of their relative attractiveness with that of one or more plants listed in the Summary. Let us say that, on the basis of three tests with a species of Orthoptera, we find that 9 / 3 / 15 / 8, and that the results of a fourth test are as follows: Test IV. 9 / 3 / 21 / 8.

On the basis of incomplete data, we can assume that plant 21 belongs near 15 in its preference value, for, like 15, it is less acceptable than plants 9 and 3 but more acceptable than 8. Its exact preference value cannot be determined, of course, without further testing.

TABLE III[23]

Classification and Distribution of Structural Adaptations of Mouthparts of Orthoptera — Groups and Species / Mouthpart Adaptations	Carnivorous	Forbivorous-seminivorous-carnivorous	Seminivorous	Modified Omnivorous	Omnivorous	Omnivorous toward forbivorous	Dendrophagous	Forbivorous toward dendrophagous	Forbivorous	Forbivorous toward herbivorous	Herbivorous toward forbivorous	Herbivorous	Herbivorous toward graminivorous	Graminivorous toward herbivorous	Graminivorous
Dermaptera:															
Doru a. aculeatum					X										
Blattidae:															
Blatta orientalis					X										
Blattella germanica					X										
Parcoblatta uhleriana					X										
Parcoblatta virginica					X										
Mantidae:															
Tenodera aridifolia sinensis	X														
Phasmidae:															
Diapheromera femorata							X								
Acridinae:															
Chloealtis conspersa															X
Chorthippus longicornis															X
Orphulella speciosa															X
Pseudopomala brachyptera															X
Syrbula admirabilis															X
Oedipodinae:															
Arphia p. pseudonietana															X
Arphia sulphurea															X
Camnula pellucida												X			
Chortophaga viridifasciata												X			
Dissosteira carolina															X

[23]Based largely on mandibular form. See pp. 79 - 81 for a brief discussion of the following structural adaptations.

TABLE III (CONT.)

Classification and Distribution of Structural Adaptations of Mouthparts of Orthoptera / Groups and Species / Mouthpart Adaptations	Carnivorous	Forbivorous-seminivorous-carnivorous	Seminivorous	Modified Omnivorous	Omnivorous	Omnivorous toward forbivorous	Dendrophagous	Forbivorous toward dendrophagous	Forbivorous	Forbivorous toward herbivorous	Herbivorous toward forbivorous	Herbivorous	Herbivorous toward graminivorous	Graminivorous toward herbivorous	Graminivorous
Oedipodinae, cont.:															
Encoptolophus s. sordidus															X
Pardalophora apiculata												X			
Pardalophora haldemanii												X			
Spharagemon b. bolli												X			
Spharagemon collare												X			
Cyrtacanthacridinae:															
Appalachia arcana									X						
Dendrotettix quercus												X			
Leptysma marginicollis															X
Melanoplus angustipennis									X						
Melanoplus b. bilituratus											X				
Melanoplus bivittatus												X			
Melanoplus confusus												X			
Melanoplus f.-r. femur-rubrum									X						
Melanoplus keeleri luridus									X						
Melanoplus p. punctulatus									X						
Melanoplus s. scudderi											X				
Paroxya hoosieri										X					
Phoetaliotes nebrascensis													X		
Schistocerca lineata											X				
Zubovskya g. canadensis										X					
Tetrigidae:															
Tetrix ornata					X										
Tetrix subulata					X										
Tettigidea l. lateralis					X										

TABLE III (CONT.)

Classification and Distribution of Structural Adaptations of Mouthparts of Orthoptera Groups and Species / Mouthpart Adaptations	Carnivorous	Forbivorous-seminivorous-carnivorous	Seminivorous	Modified Omnivorous	Omnivorous	Omnivorous toward forbivorous	Dendrophagous	Forbivorous toward dendrophagous	Forbivorous	Forbivorous toward herbivorous	Herbivorous toward forbivorous	Herbivorous	Herbivorous toward graminivorous	Graminivorous toward herbivorous	Graminivorous
Rhaphidophorinae:															
Ceuthophilus brevipes				X											
Ceuthophilus meridionalis				X											
Ceuthophilus thomasi				X											
Ceuthophilus uhleri				X											
Phaneropterinae:															
Amblycorypha oblongifolia									X						
Amblycorypha rotundifolia									X						
Scudderia c. curvicauda									X						
Scudderia f. furcata									X						
Scudderia septentrionalis									X						
Copiphorinae:															
Neoconocephalus ensiger			X												
Conocephalinae:															
Conocephalus attenuatus		X													
Conocephalus brevipennis		X													
Conocephalus f. fasciatus		X													
Conocephalus nigropleurum		X													
Conocephalus strictus		X													
Orchelimum gladiator		X													
Orchelimum nigripes		X													
Orchelimum volantum		X													
Orchelimum vulgare		X													
Decticinae:															
Atlanticus testaceus	X														

TABLE III (CONT.)

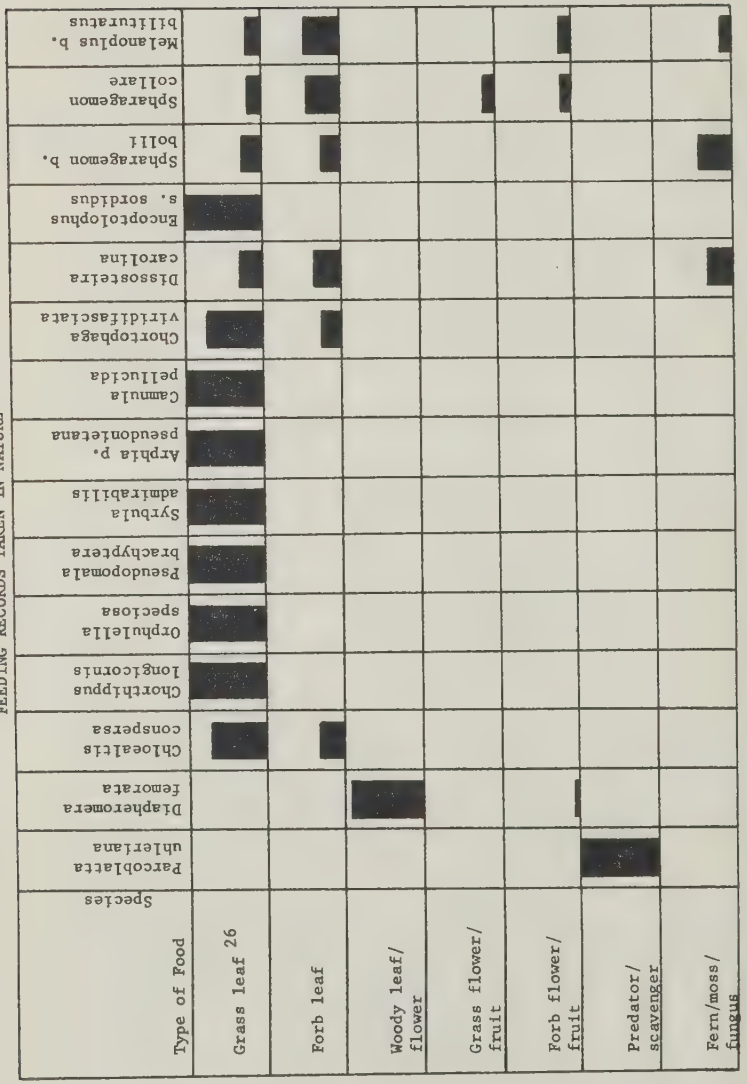
Classification and Distribution of Structural Adaptations of Mouthparts of Orthoptera / Groups and Species	Mouthpart Adaptations	Carnivorous	Forbivorous-seminivorous-carnivorous	Seminivorous	Modified Omnivorous	Omnivorous	Omnivorous toward forbivorous	Dendrophagous	Forbivorous toward dendrophagous	Forbivorous	Forbivorous toward herbivorous	Herbivorous toward forbivorous	Herbivorous	Herbivorous toward graminivorous	Graminivorous toward herbivorous	Graminivorous
Gryllinae:																
Acheta pennsylvanicus							X									
Nemobiinae:																
Nemobius allardi							X									
Oecanthinae:																
Oecanthus angustipennis					X											
Gryllotalpidae:																
Gryllotalpa hexadactyla					X											

TABLE IV [24]
SUMMARY OF PRIMARY AND SECONDARY FOOD-HABITS OF ORTHOPTERA, BASED ON PRESENT STUDIES SUPPLEMENTED BY LITERATURE

Groups	Primary Food-Habits	Secondary Food-Habits
Dermaptera	Omnivorous or omnivorous-carnivorous	
Blattidae	Omnivorous	
Mantidae	Carnivorous	
Phasmidae	Dendrophagous	
Acridinae	Graminivorous	
Oedipodinae	Graminivorous	Forbivorous
Cyrtacanthacridinae	Forbivorous or forbivorous-graminivorous	Dendrophagous
Tetrigidae	Omnivorous-herbivorous	
Rhaphidophorinae	Omnivorous or omnivorous-carnivorous	
Phaneropterinae	Forbivorous	Dendrophagous
Copiphorinae	Seminivorous	
Conocephalinae	Forbivorous-seminivorous-carnivorous	
Decticinae	Omnivorous-carnivorous	
Gryllinae & Nemobiinae	Omnivorous or omnivorous-herbivorous	Carnivorous
Oecanthinae	Forbivorous-carnivorous	Dendrophagous
Gryllotalpidae	Omnivorous	Carnivorous

[24] Based on the discussion presented on pp.81-113. It summarizes the author's impressions of food selection in a majority of the species of each of the following groups and ignores variations of food-habit which may occur in certain species.

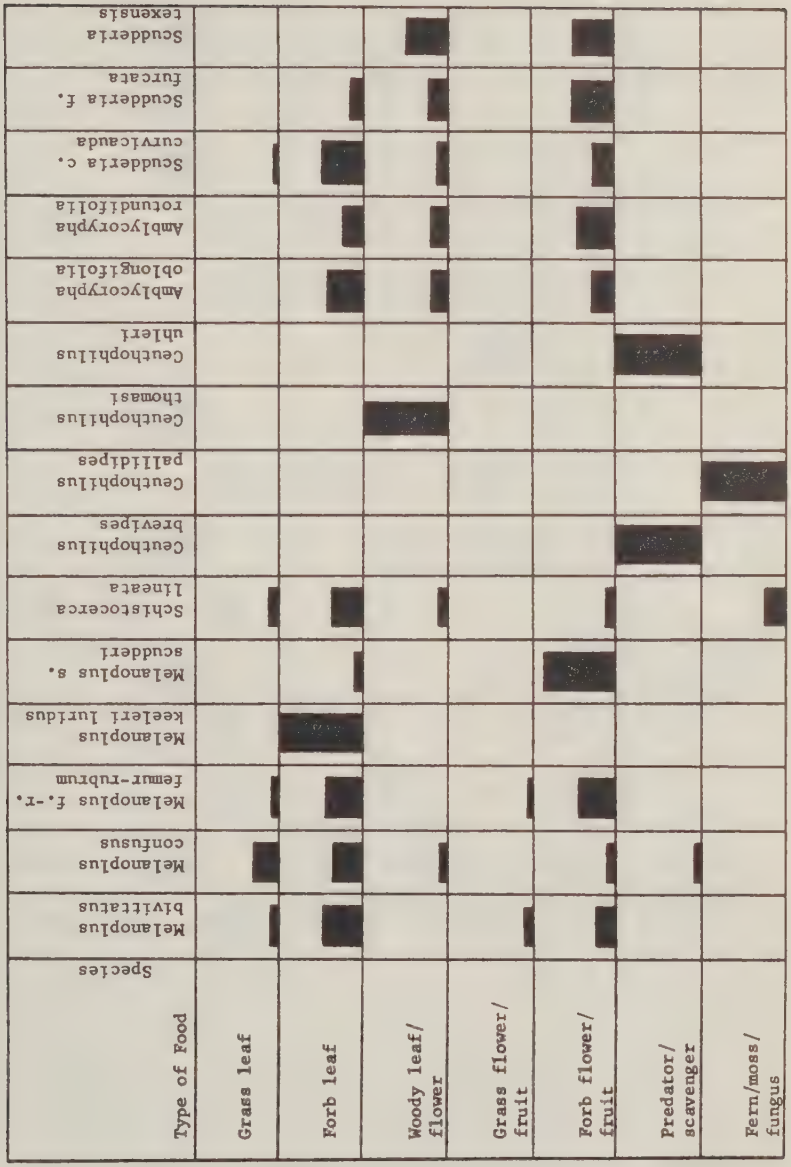
GRAPH I 25
FEEDING RECORDS TAKEN IN NATURE



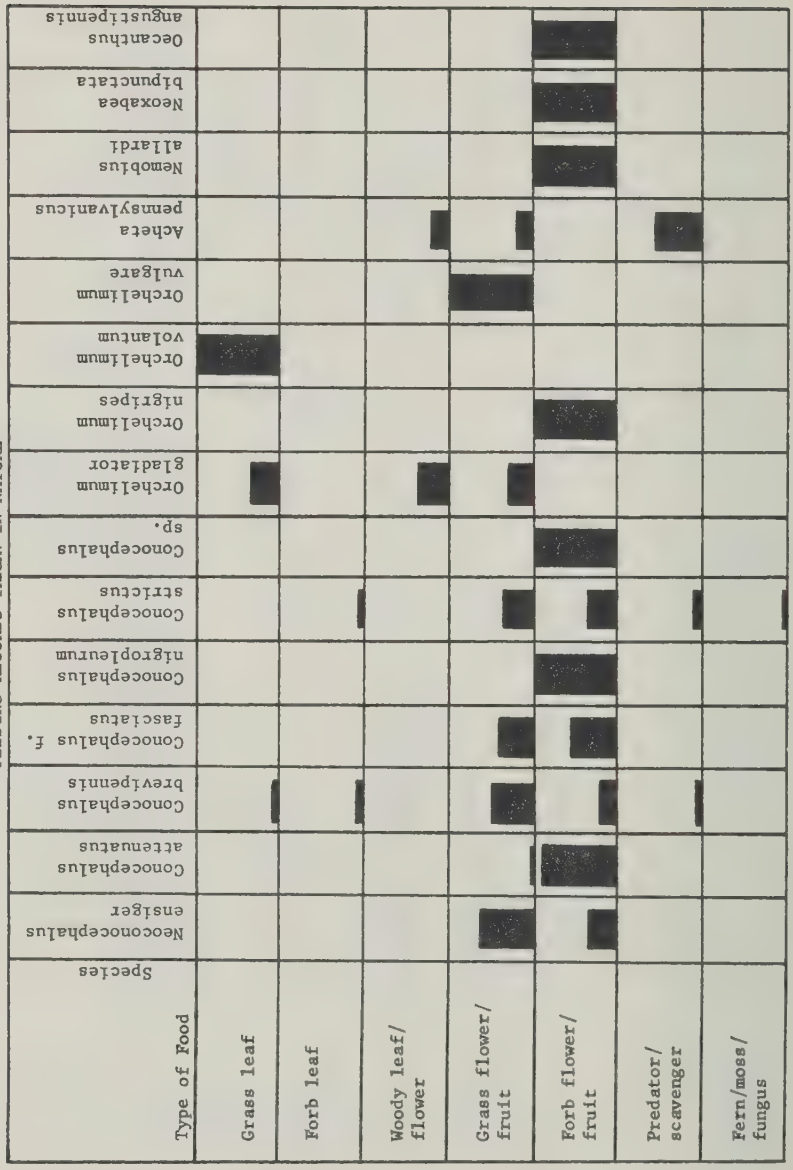
25 The feeding records obtained during this study and presented in their entirety in Table I are here reworked on the basis of food categories. The height of each bar corresponds to the percentage of feeding observed in that given category; thus, examination of the graph shows that Chortophaga was found eating grass leaves 75% of the time, the remainder of the time feeding on forb leaves.

26 The term grass, as loosely used here, refers to plants of the Gramineae, Cyperaceae, and Juncaceae.

GRAPH I (CONT.)
FEEDING RECORDS TAKEN IN NATURE



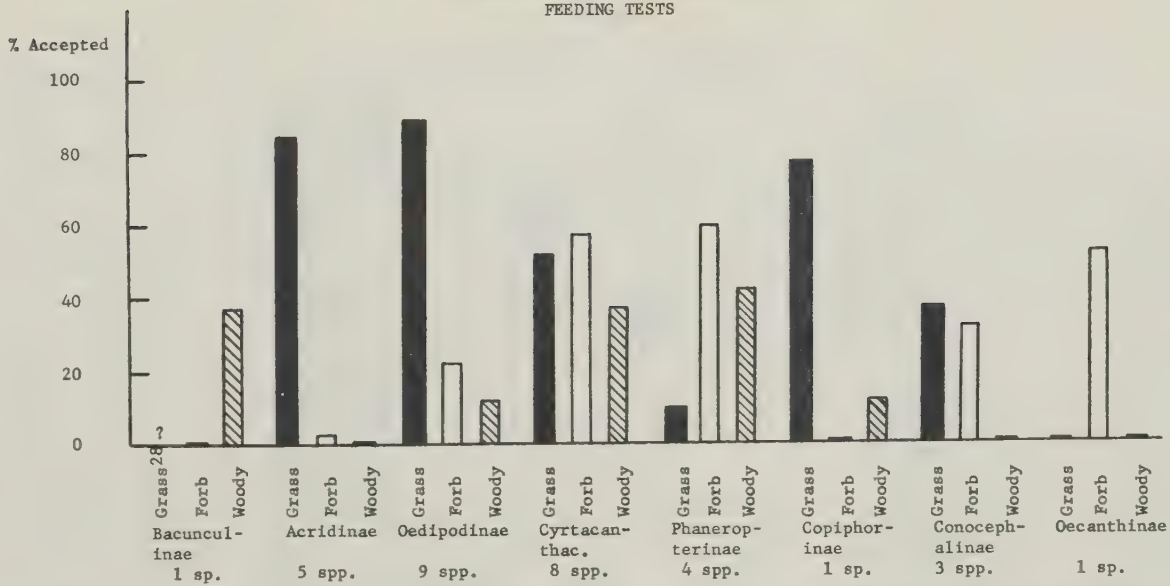
GRAPH I (CONT.)
FEEDING RECORDS TAKEN IN NATURE



GRAPH I (CONT.)
FEEDING RECORDS TAKEN IN NATURE

Type of Food / Species	Oecanthus latipennis	Oecanthus n. nigricornis	Oecanthus n. quadripunctatus	Oecanthus niveus	Anaxipha exigua
Grass leaf					
Forb leaf					
Woody leaf/ flower					
Grass flower/ fruit					
Forb flower/ fruit					
Predator/ scavenger					
Fern/moss/ fungus					

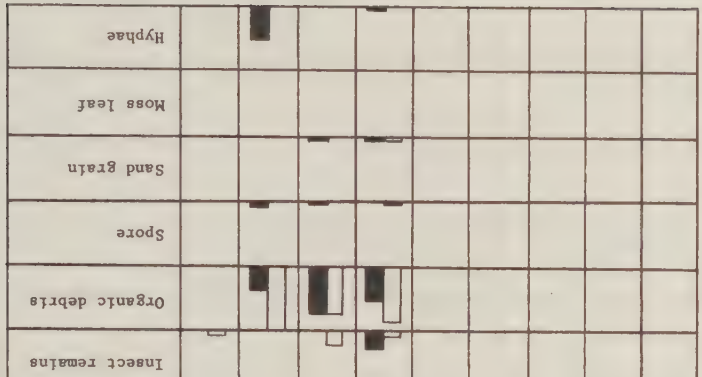
GRAPH II [27]
RELATIVE ACCEPTANCE OF FOODS BY SUBFAMILIES
OF ORTHOPTERA DURING DIFFERENTIAL
FEEDING TESTS



[27] Graph II shows the relative acceptance of plants belonging to woody, forb, and grass categories by species of Orthoptera grouped taxonomically. The following steps are involved in its formulation: for grasses, the number of acceptances and that of rejections and nibbling during the differential feeding tests is counted for a given species of feeder, and this information is used to calculate the percentage of acceptance of grasses by this orthopteran. The percentage of acceptance of grasses is then determined in the same manner for the remainder of the species of this subfamily of Orthoptera, and these percentages are averaged to yield a mean percentage of acceptance of grasses for the subfamily. This procedure is repeated to determine the percentage of acceptance of forbs and then of woody plants. The remaining subfamilies are then treated in the same manner. The cross-hatched bars denote acceptance of woody plants, the solid bars that of grasses, and the empty bars that of forbs. The height of each bar indicates the percentage of acceptance. The number of species tested appears below each subfamily name.

[28] The term grass, as loosely used here, refers to plants of the Gramineae, Cyperaceae, and Juncaceae.

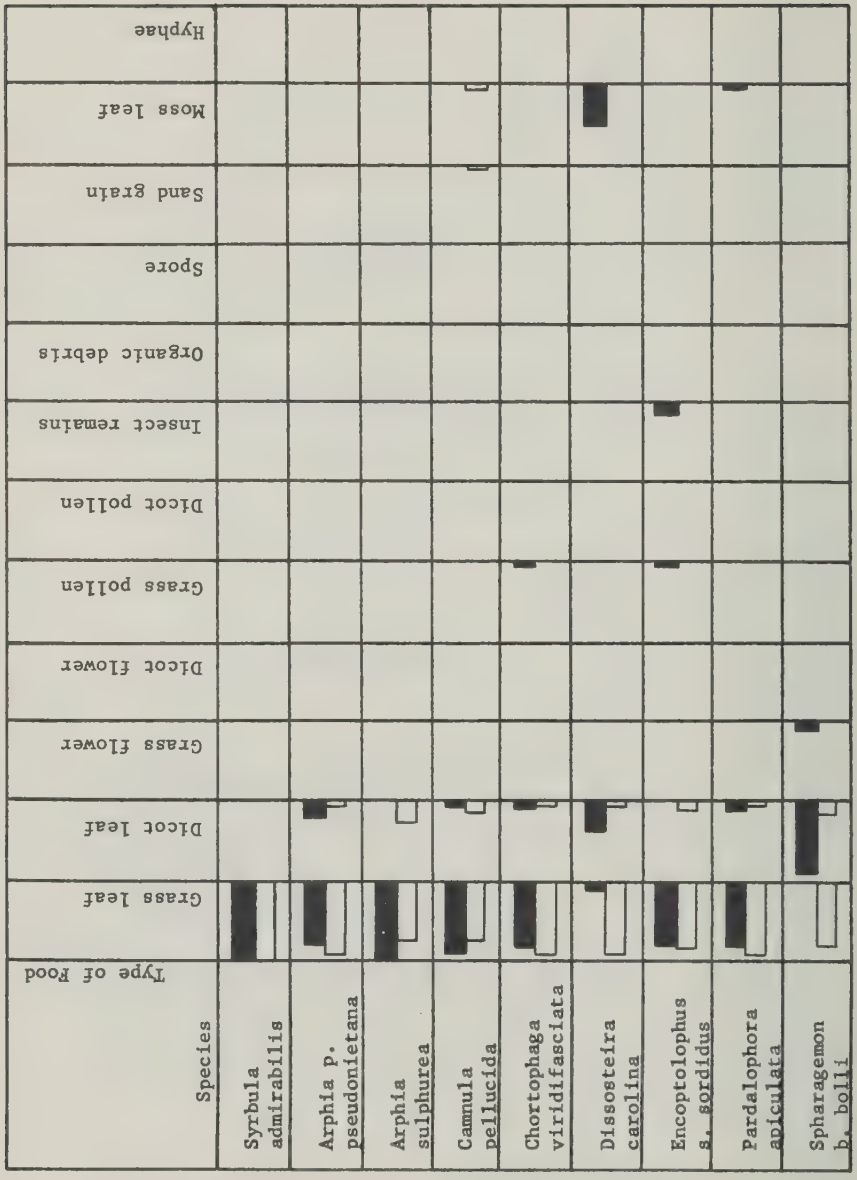
GRAPH III 29
RESULTS OF ANALYSES OF CROP CONTENTS
AND FECAL MATERIALS



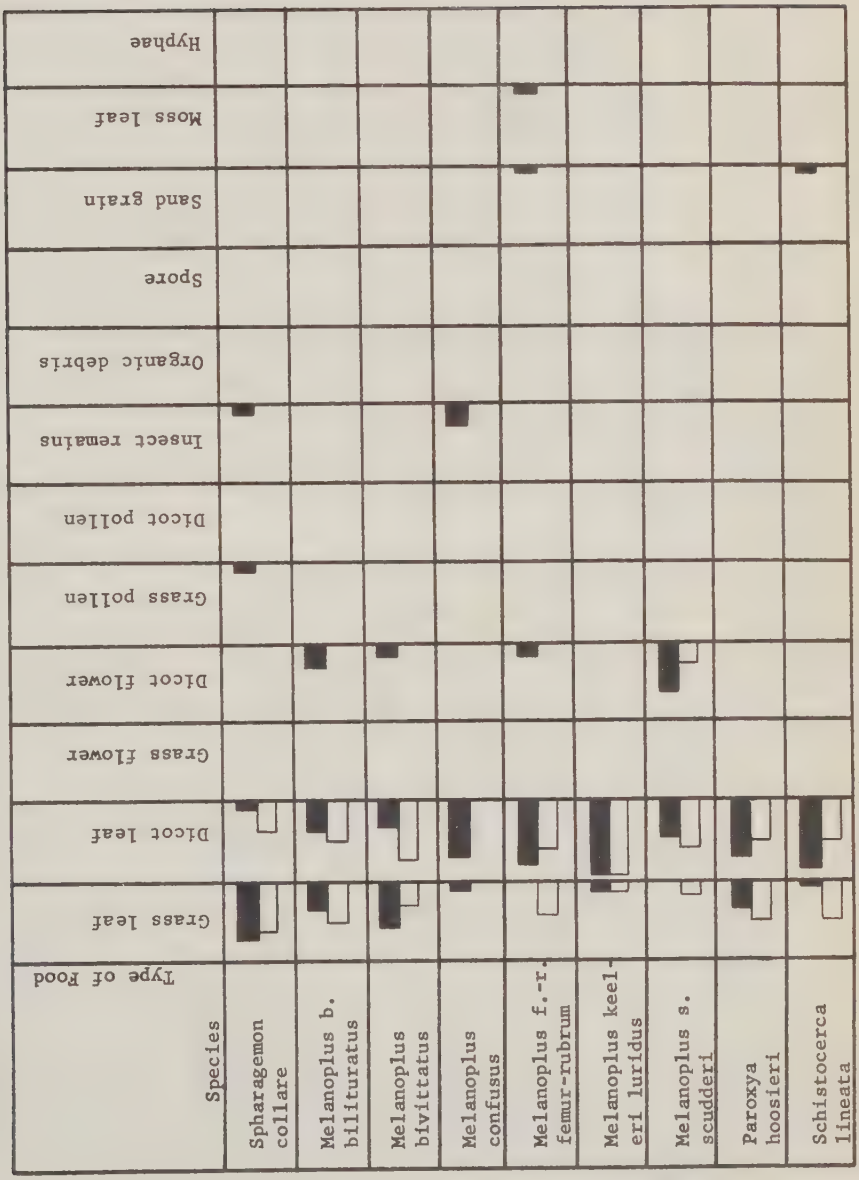
29 The composition of the crop contents and fecal materials of Orthoptera examined during this study is summarized in Graph III. A solid bar denotes data from crop analyses and an empty bar that from fecal analyses. The height of each bar shows the estimated percentage of the content belonging in a given food category; for example, 100% of both the crop contents and the fecal materials of Diapheromera femorata were of dicot leaf origin. See pp.79 - 80 for a brief discussion of the techniques of analysis.

30 The term grass, as loosely used here, refers to plants of the Gramineae, Cyperaceae, and Juncaceae.

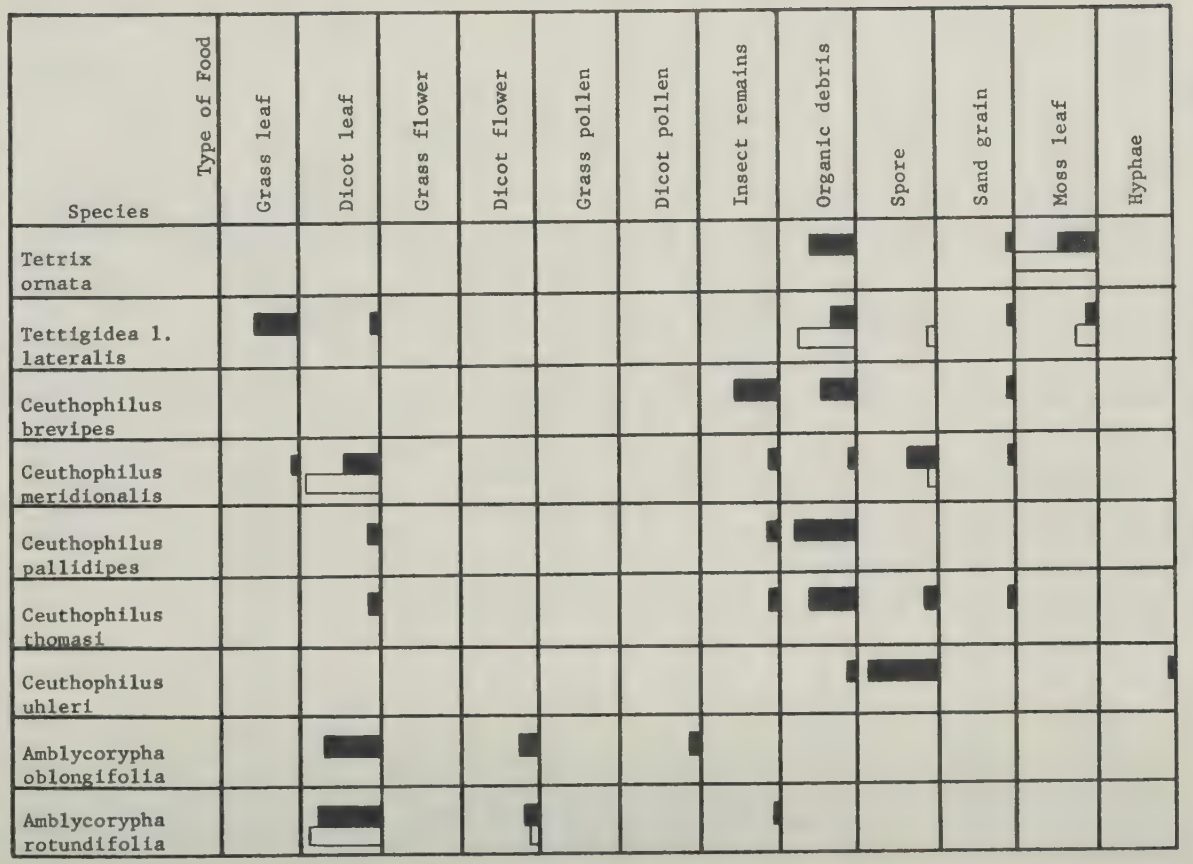
GRAPH III (CONT.)
RESULTS OF ANALYSES OF CROP CONTENTS
AND FECAL MATERIALS



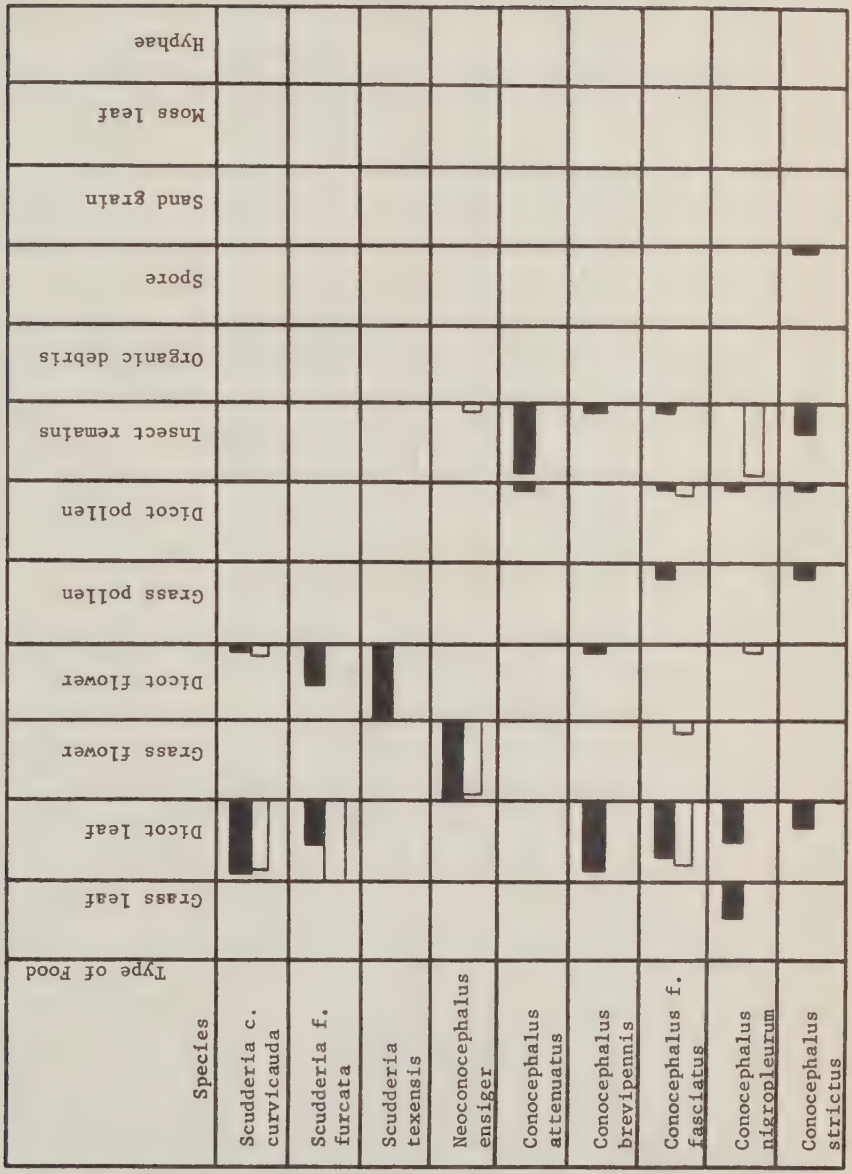
GRAPH III (CONT.)
RESULTS OF ANALYSES OF CROP CONTENTS
AND FECAL MATERIALS



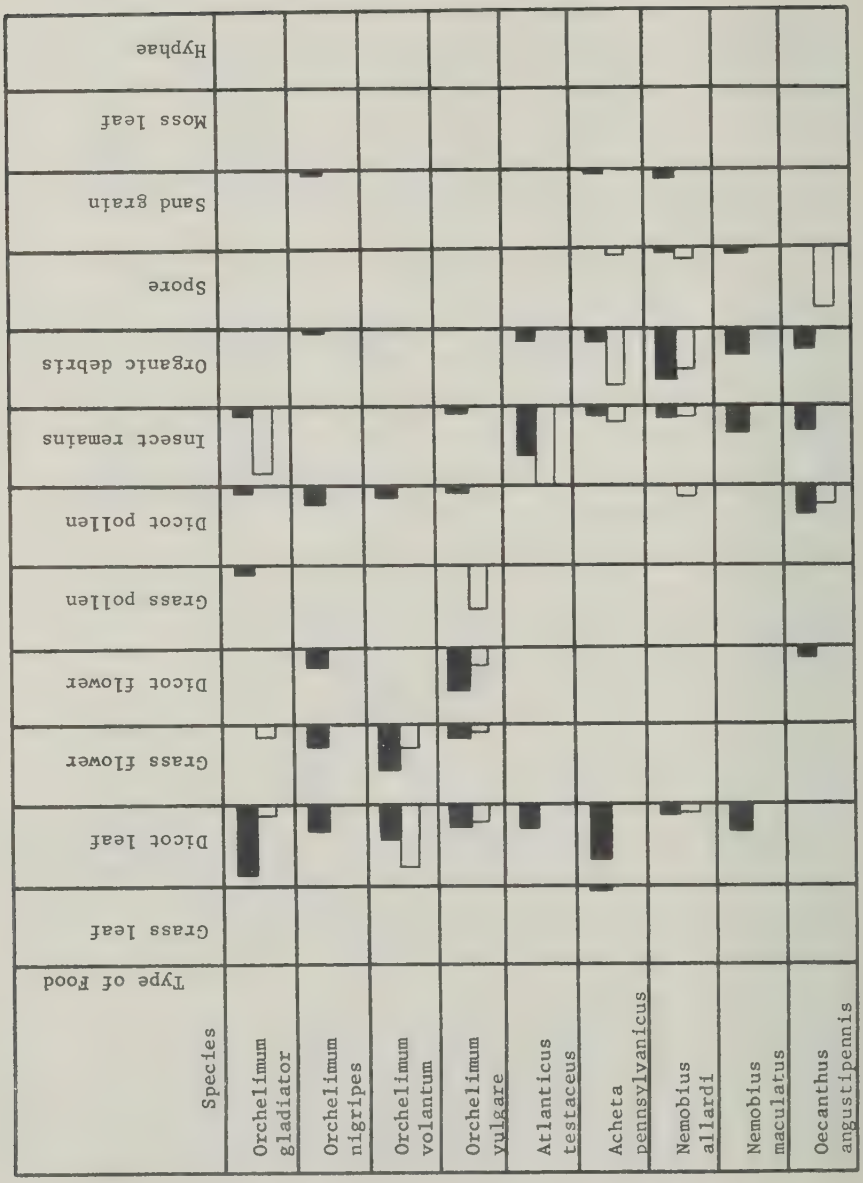
GRAPH III (CONT.)
RESULTS OF ANALYSES OF CROP CONTENTS
AND FECAL MATERIALS



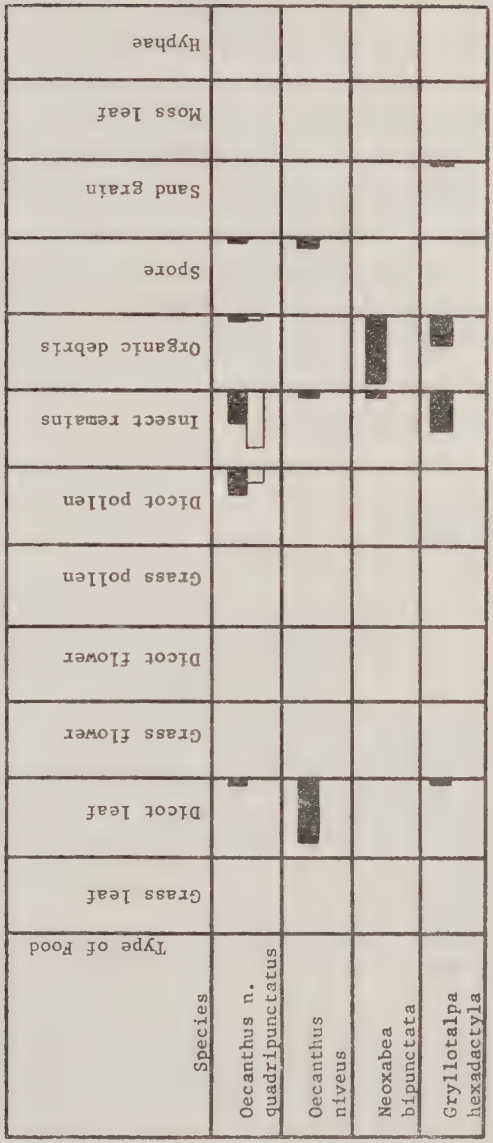
GRAPH III (CONT.)
RESULTS OF ANALYSES OF CROP CONTENTS
AND FECAL MATERIALS



GRAPH III (CONT.)
RESULTS OF ANALYSES OF CROP CONTENTS
AND FECAL MATERIALS



GRAPH III (CONT.)
RESULTS OF ANALYSES OF CROP CONTENTS
AND FECAL MATERIALS



APPENDIX A

GROUPS AND SPECIES OF ORTHOPTERA STUDIED

The preceding report deals with food selection in seventy-six species and subspecies of Orthoptera [31] occurring in Michigan—about one-half of the total number known from the entire state. Among these are representatives of every suborder and family found in Michigan, as well as most of the families occurring in the United States. Except at the onset of the investigation, when Dr. T. H. Hubbell kindly assisted in the determination of certain difficult specimens, the author made all determinations by reference to standard works and comparison with identified material in the collections of the University of Michigan Museum of Zoology. The species studied and their current classification are shown in the following list:

Order DERMAPTERA (earwigs)

Forficulidae (earwigs)
- Forficulinae
  - *Doru a. aculeatum* (Scudder)

Superorder ORTHOPTEROIDEA
("*ORTHOPTERA*" sens. lat.)
Order OÖTHECARIA

Blattidae sens. lat. or Blattodea (cockroaches)
- Pseudomopinae
  - *Blattella germanica* (Linnaeus)
  - *Parcoblatta pensylvanica* (DeGeer)
  - *Parcoblatta uhleriana* (Saussure)
  - *Parcoblatta virginica* (Brunner)
- Blattinae
  - *Blatta orientalis* Linnaeus
- Blaberinae
  - *Byrsotria fumigata* (Guerin) [32]

Mantidae sens. lat. or Mantodea (praying mantids)
- Mantinae
  - *Tenodera aridifolia sinensis* Saussure

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[31] The term Orthoptera, which is here used loosely, includes insects belonging to the orders Orthoptera and Dermaptera, both of which are customarily studied by orthopterists.

[32] Not a native species.

Order PHASMIDA or PHASMODEA (walking-sticks)

Phasmidae sens. lat. or Phasmida
Bacunculinae
Diapheromera femorata (Say)

Order SALTATORIA

Suborder COELIFERA

Superfamily ACRIDOIDEA

Acrididae (short-horned grasshoppers)
Acridinae (slant-faced locusts)
Chloealtis conspersa Harris
Chorthippus longicornis (Latreille)
Orphulella speciosa (Scudder)
Pseudopomala brachyptera (Scudder)
Syrbula admirabilis (Uhler)
Oedipodinae (band-winged locusts) [33]
Arphia p. pseudonietana (Thomas)
Arphia sulphurea (Fabricius)
Camnula pellucida (Scudder)
Chortophaga viridifasciata (DeGeer)
Dissosteira carolina (Linnaeus)
Encoptolophus s. sordidus (Burmeister)
Pardalophora apiculata (Harris)
Pardalophora haldemanii (Scudder)
Spharagemon b. bolli Scudder
Spharagemon collare (Scudder)
Cyrtacanthacridinae (spine-breasted locusts)
Appalachia arcana Hubbell and Cantrall
Dendrotettix quercus Packard
Leptysma marginicollis (Serville)
Melanoplus a. angustipennis (Dodge)
Melanoplus b. bilituratus (F. Walker)
Melanoplus bivittatus (Say)
Melanoplus confusus Scudder
Melanoplus f.-r. femur-rubrum (DeGeer)
Melanoplus keeleri luridus (Dodge)
Melanoplus p. punctulatus (Scudder)
Melanoplus s. scudderi (Uhler)
Paroxya hoosieri (Blatchley)
Phoetaliotes nebrascensis (Thomas)
Schistocerca lineata Scudder
Zubovskya glacialis canadensis (E. M. Walker)

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[33] See footnote 9.

TETRIGIDAE (GROUSE LOCUSTS)
Tetrix ornata (Say)
Tetrix subulata (Linnaeus)
Tettigidea l. lateralis (Say)

SUBORDER ENSIFERA

SUPERFAMILY TETTIGONOIDEA

GRYLLACRIDIDAE
RHAPHIDOPHORINAE (CAVE AND CAMEL CRICKETS)
Ceuthophilus brevipes Scudder
Ceuthophilus meridionalis Scudder
Ceuthophilus pallidipes Walker
Ceuthophilus thomasi Hubbell
Ceuthophilus uhleri Scudder
TETTIGONIIDAE
PHANEROPTERINAE (BUSH AND ROUND-HEADED KATYDIDS)
Amblycorypha oblongifolia (DeGeer)
Amblycorypha rotundifolia (Scudder)
Scudderia c. curvicauda (DeGeer)
Scudderia f. furcata Brunner
Scudderia septentrionalis (Serville)
Scudderia texensis Saussure and Pictet
COPIPHORINAE
Neoconocephalus ensiger (Harris)
CONOCEPHALINAE (MEADOW GRASSHOPPERS)
Conocephalus attenuatus (Scudder)
Conocephalus brevipennis (Scudder)
Conocephalus f. fasciatus (DeGeer)
Conocephalus nigropleurum (Bruner)
Conocephalus strictus (Scudder)
Orchelimum gladiator (Bruner)
Orchelimum nigripes (Scudder)
Orchelimum volantum McNeill
Orchelimum vulgare Harris
DECTICINAE (SHIELD-BEARERS)
Atlanticus testaceus (Scudder)

SUPERFAMILY GRYLLOIDEA

GRYLLIDAE
GRYLLINAE (FIELD CRICKETS)
Acheta pennsylvanicus (Burmeister)
Acheta domesticus (Linnaeus)
NEMOBIINAE (GROUND CRICKETS)
Nemobius allardi Alexander and Thomas
Nemobius maculatus Blatchley

OECANTHINAE (WHITE TREE CRICKETS)
Neoxabea bipunctata (DeGeer)
Oecanthus angustipennis Fitch
Oecanthus latipennis Riley
Oecanthus n. nigricornis F. Walker
Oecanthus n. quadripunctatus Beutenmüller
Oecanthus niveus (DeGeer)
TRIGONIDIINAE (WINGED BUSH CRICKETS)
Anaxipha exigua (Say)
GRYLLOTALPIDAE (MOLE CRICKETS)
Gryllotalpa hexadactyla Perty

APPENDIX B
HABITATS STUDIED

Ann Arbor, a city approximately 45 miles west of Detroit, Michigan, is located in Washtenaw County on the banks of the Huron River in southeastern Michigan. The city is situated in a region of smooth to moderately hilly glacial terrain, except where it is cut by the rather broad, deep valley of the Huron River. The uplands immediately south of the Huron River are ground moraine and glacial outwash; those to the north predominately kames; and the river borders are alluvium and river terraces (U. S. D. A. *Yearbook,* 1938). The soils of Ann Arbor and the outlying districts are loams of the Miami-Crosby-Brookston soil association (U. S. D. A. Soil Survey Washtenaw County, Mich.). Marshes occur near the river margins at elevations of approximately 740 to 780 feet above sea level. The elevation of the uplands generally ranges from 800 to 900 feet. All uplands are cleared and used for housing or industry, except for scattered fields near the outskirts of the city.

Observations were carried out at many different points in the outskirts of the city and beyond, but much time was spent at the conveniently located Nichols Arboretum, which contains the only remaining wooded areas of fair size. The Arboretum is located on the eastern border of Ann Arbor, adjacent to the Huron River. While its wooded areas are not virgin, they are comparatively untouched.

The Edwin S. George Reserve is located about 25 miles northwest of Ann Arbor in the southwestern corner of Livingston County, which is situated in the Miami-Kewaunee soil area (U. S. D. A. *Yearbook,* 1938). The soils of the Reserve are loams, mucks, and peats (U. S. D. A. Soil Survey Livingston County, Mich.). Most of the land below 900 feet of elevation is swampy, generally being covered by shrub-sedge, grass-sedge-fern, or tamarack marshes, but sometimes by hardwood swamps or sphagnum-leatherleaf bogs. The uplands above 915 feet consist of scattered dry fields and hardwood forests not unlike the original oak-hickory forest cleared by the settlers.

Cantrall (1943) discussed the soils, weather, and other environmental factors of the Reserve in his superb ecologic study

of the Orthoptera of the area, and Evans and Dahl (1955) recently summarized its weather conditions. Numerous papers describing various aspects of the Reserve's fauna and its ecology have been published. Anyone desiring additional information may turn to these works.

This appendix contains descriptions of many of the stations studied during the course of this investigation, each of which consists of a complex of habitats. It was necessary to make a compromise between economy and complete description. Therefore, only eleven of the most-visited stations are described in some detail; less-frequently visited ones which are the sites of feeding records are briefly described; and all others are omitted.

Each of the eleven detailed discussions includes: (1) comments on location, habitat type, surrounding areas, dominant plants, topography, soil, elevation, and other relevant material; (2) a list of plants subjectively grouped according to abundance; (3) a list of Orthoptera. These lists are not complete but merely include the more prominent and characteristic species seen during successive visits to the stations. They are valuable because they help to characterize the habitat of each station and because they serve as a basis by which feeding records may be evaluated in terms of relative abundance of food-plants.

In view of the great differences in behavior and in habitat selection among the Orthoptera of a given community, a ranking of plant species according to abundance, hence, availability for feeding, is necessarily true for a majority of the Orthoptera, but not for all. The following example will illustrate this point.

Scudderia septentrionalis, a Michigan katydid, is a tree-dweller, whereas a related species, *S. c. curvicauda,* is an inhabitant of the shrub-forb stratum of the same woods. *S. septentrionalis* will accept certain forbs, but these plants are not available in the arboreal stratum in which it normally lives. *S. c. curvicauda,* in contrast, eats flowers and leaves of forbs but seldom eats tree leaves and does not show much liking for them when they are available. Obviously, the significance of the abundance of woody plants of a station differs for *S. septentrionalis* and *S. c. curvicauda.* The same is true for the abundance of forbs or of any of the other kind of food-plant.

Several rather arbitrary criteria were used in the evaluation of plant abundance. So-called *abundant* species are those which occur throughout the community and are sufficiently available for a species to feed exclusively on them; also classed as abundant are those plants which are localized in an almost pure stand composing a fairly large portion of a community, though they are not available throughout the community. *Common* plants are those observed at frequent to infrequent intervals whenever one walks slowly through a community. If a species were restricted to such a food-plant, its individuals might occasionally experience difficulty in finding food, but would not starve. *Uncommon* plants, species so scarce that they might not be seen when one walks through the community, would be unable to support a large population monophagous on them. For this reason, uncommon plants have been omitted from the following lists of abundance of plant species.

The Orthoptera listed as occurring in the stations are not necessarily characteristic of the habitats there represented. Some of them, the " erratics " of Cantrall (1943), are individuals which have wandered from their characteristic habitat and are unable to reproduce in the new situation. An example is the anomalous occurrence of the walking-stick *Diapheromera femorata,* a woodland form, in a marsh (Station 28D). The several walking-sticks found in the marsh must have fallen from the overhanging trees into the marsh border, a situation totally foreign to them.

A detailed description of certain frequently visited stations and a very general one of less-visited stations follows.

Station 4A.—Field between the Huron River and Geddes Road, closely adjacent to Geddes Bridge, Ann Arbor area. This is a former pasture now choked with dense growths of *Rhus.* The habitat is similar to that of Station 17A.

Station 5.—Marsh near the northeastern border of the junction of Michigan Highway 17, United States Highway 23, and Hog Back Road, Ann Arbor area. This is a forb-sedge-grass marsh with large amounts of *Leersia* and *Typha.* The habitat is similar to that of Station 25.

Station 6.—Field directly southeast of the junction of Stadium Boulevard (Highway 17) and Washtenaw Avenue, Ann Arbor.

The edges of this meadow are contiguous with a small stand of hardwoods. The field is dominated by *Phleum,* but its field-wood ecotone is rather mesic, supporting a good growth of *Fragaria, Podophyllum,* and *Viola.* The habitat is rather similar to that of Station 13.

Station 8.—Woods to the east of Service Road, Arboretum, Ann Arbor.[34] This rather mesic oak-hickory woods is traversed by foot paths and bounded by roads and open fields. At its margins, where the woods is lower and somewhat open, there grows a profusion of shrubs, forbs, and scattered trees. At the more heavily wooded summit there is a patch of *Pinus.* Most of the woods is dominated by oak trees, which form a distinct canopy. In the more shaded places the floor is covered by *Carex pensylvanica* and various forbs. *Aster* spp., *Poa Compressa, Solidago* spp., and small shrubs grow along the path margins. This luxurious growth of forbs is in distinct contrast to that seen in the

Abundant [35]

Carex pensylvanica
Cornus stolonifera
Hamamelis virginiana
Lonicera canadensis
Pinus sp.
Poa compressa
Quercus rubra
Quercus velutina
Solidago caesia

Common [35]

Anemone virginiana
Aster laevis
Aster lateriflorus
Aster sagittifolius
Carpinus caroliniana
Carya glabra

Common (Cont.)

Carya ovata
Corylus americanus
Crataegus spp.
Helianthus divaricatus
Juglans nigra
Lonicera tatarica
Monarda fistulosa
Panicum sp.
Prunus serotina
Prunus virginiana
Quercus alba
Rhamnus alnifolia
Rhus typhina
Rubus occidentalis
Solidago canadensis
Vitis riparia

[34] Those parts of the Arboretum and the George Reserve having well-established names will be cited accordingly.

[35] See pp. 210 and 163–164 for a discussion of abundant and common species.

more xeric woods of the Reserve. Leaf litter is several inches in thickness. The elevation extends from about 800 to 840 feet. The soil is Bellefontaine sandy loam.

The relative abundance of the more prominent plants of Station 8 is given above (p. 211).

The following is a list of the Orthoptera observed at Station 8:

Amblycorypha oblongifolia
Amblycorypha rotundifolia
Ceuthophilus brevipennis
Ceuthophilus divergens
Ceuthophilus meridionalis
Ceuthophilus pallidipes
Ceuthophilus thomasi
Diapheromera femorata
Melanoplus s. scudderi
Nemobius maculatus
Nemobius tinnulus
Neoconocephalus ensiger
Neoxabea bipunctata
Oecanthus angustipennis
Oecanthus niveus
Parcoblatta uhleriana
Scudderia c. curvicauda
Scudderia f. furcata
Scudderia septentrionalis

Station 10.—Field to the west of the junction between United States Highway 23 and Dhu Varren Road, Ann Arbor area. A new housing development is encroaching on this small shrubby field, which is choked by a thick growth of many forbs, especially *Solidago* spp., and shrubs, especially *Rhus*. The habitat is similar to that of Station 17A.

Station 11.—Woods to the northwest of Glen Drive, immediately north of Heathdale, Arboretum, Ann Arbor. This is an oak-hickory woods with a well-developed shrub and forb stratum. *Aster macrophyllus, Collinsonia, Desmodium glutinosum,* and *Podophyllum* are some of the common forbs. The habitat is rather similar to that of Station 8.

Station 12.—Field between the intersection of Glen Drive and Locust Knob, Arboretum, Ann Arbor. This field is bounded by low, wooded hills. Approximately one-half of it is low and level, supporting a rather luxurious growth of forbs and grasses, mostly *Dactylis, Plantago,* and *Poa*. The other half is high and rather dry, supporting a more arid type of vegetation, the dominant plants of which are *Achillea, Eragrostis, Panicum,* and *Setaria*. The habitat is similar to that of Station 13.

Station 13.—Field bisected by the Service Road, Arboretum, Ann Arbor. This open field is surrounded by higher, wooded

areas. Two-thirds of the field is low, supporting vegetation of the wet-field type; the remaining one-third is hilly, somewhat higher and drier, and its vegetation tends toward the dry-field type. *Achillea, Plantago, Poa,* and *Setaria* dominate the hilly area, in contrast to the rather rich growth of *Danthonia, Fragaria, Plantago, Poa,* and *Trifolium* in the lower, flat area. The field is disturbed by regular mowing. Its elevation is approximately 820 to 880 feet, and its soil is Bellefontaine sandy loam.

The relative abundance of the more prominent plants of Station 13 is as follows:

Abundant

Achillea millefolium
Dactylis glomerata
Danthonia spicata
Fragaria virginiana
Panicum sp.
Plantago major
Plantago rugelii
Poa pratensis
Setaria glauca
Trifolium repens

Common

Ambrosia artemisiifolia
Aster laevis
Aster sagittifolius
Bromus inermis

Common (Cont.)

Eragrostis spectabilis
Erigeron strigosus
Juncus tenuis
Linaria vulgaris
Medicago lupulina
Oxalis stricta
Phleum pratense
Poa compressa
Potentilla recta
Prunella vulgaris
Rudbeckia serotina
Solidago nemoralis
Taraxacum officinale
Trifolium pratense
Viola papilionacea

The following is a list of the Orthoptera observed at Station 13:

Acheta pennsylvanicus
Amblycorypha rotundifolia
Arphia sulphurea
Chloealtis conspersa
Chorthippus longicornis
Chortophaga viridifasciata
Conocephalus brevipennis
Conocephalus f. fasciatus
Conocephalus strictus
Dissosteira carolina
Encoptolophus s. sordidus
Melanoplus bivittatus
Melanoplus confusus
Melanoplus f.-r. femur-rubrum

Orthoptera at Station 13 (Cont'd.):

Melanoplus keeleri luridus
Melanoplus s. scudderi
Nemobius allardi
Neoconocephalus ensiger
Oecanthus angustipennis
Orphulella speciosa
Scudderia c. curvicauda
Scudderia f. furcata
Spharagemon b. bolli
Syrbula admirabilis
Tetrix subulata
Tettigidea l. lateralis

Station 14.—Marsh adjacent to the western margin of Southwest Woods, George Reserve. The marsh is dominated by associations of sedges (especially *Carex lacustris* and *C. stricta* var. *strictior*), ferns (*Onoclea sensibilis*), and forbs (*Solidago canadensis* and *Verbena hastata*).

Station 15.—Field to the southwest of Miller Avenue, midway between Maple Road and North Seventh Street, Ann Arbor. This shrubby field with a considerable growth of *Melilotus* is now the site of a housing development.

Station 16.—Wooded bank of Liberty Creek, near Park Bridge, Liberty Park, Girard, Trumbull County, Ohio. Tangled forbs, shrubs, and grasses grow in comparative shade under the hardwoods which overlook Liberty Creek.

Station 17A.—Field to the south of the junction of Geddes Avenue and the East Huron River Drive, Ann Arbor area. This shrubby field is bordered by roads and by patches of woodland. When the present study was begun, the field was newly cleared and the vegetation not tangled, but after several years the vegetation became choked, and a primitive road leading to a housing development was built, bisecting the field. The vegetation consists largely of *Aster* spp., *Melilotus alba, Solidago canadensis,* and grasses, with many shrubs, particularly *Rhus glabra,* scattered throughout. The elevation of the station is 780 feet, and its soil is Bellefontaine sandy loam.

The relative abundance of the more prominent plants of Station 17A is as follows:

Abundant

Achillea millefolium
Aster laevis
Aster sagittifolius
Dactylis glomerata
Daucus carota
Melilotus alba
Monarda fistulosa
Poa pratensis
Rhus glabra
Solidago canadensis

Common

Agropyron repens
Ambrosia artemisiifolia

Common (Cont.)

Aster novae-angliae
Aster pilosus
Erigeron strigosus
Fragaria virginiana
Juncus tenuis
Phleum pratense
Plantago lanceolata
Poa compressa
Potentilla recta
Quercus velutina
Rhus radicans
Rubus flagellaris
Rubus occidentalis

The following is a list of the Orthoptera observed at Station 17A:

Chortophaga viridifasciata
Dissosteira carolina
Encoptolophus s. sordidus
Melanoplus confusus
Melanoplus f.-r. femur-rubrum
Melanoplus s. scudderi
Oecanthus n. nigricornis
Scudderia f. furcata

Station 17B.—Grassy margin of the Michigan Central Railroad tracks at junction with Geddes Avenue, Ann Arbor area. This gravel bank is covered by an almost pure stand of *Andropogon* but also supports some *Bromus inermis* and *Elymus.*

Station 18.—Marsh directly north of the junction of the Huron River and Tubbs Road, Ann Arbor area. This habitat is a typical Huron River marsh, supporting many shrubs, sedges, and forbs, particularly *Eupatorium* spp.

Station 21A.—Field directly northeast of Fuller Road, 0.4 miles northwest of Geddes Bridge, Ann Arbor area. This dry field is bordered by marshes, roads, and scattered patches of woodland. It is rather flat but abruptly slopes downward at the Fuller Road and marsh margins. The vegetation is mostly *Agropyron, Chrysanthemum, Equisetum* spp., *Poa* spp., and *Solidago* spp., together with scattered shrubs, particularly *Cornus,*

Ptelea, and *Prunus.* The elevation is 800 feet and the soil Bellefontaine sandy loam. In many respects this station is similar to Cantrall's mixed grass-herbaceous ones of the George Reserve.

The relative abundance of the more prominent plants of Station 21A is as follows:

Abundant	Common
Achillea millefolium	*Cornus stolonifera*
Agropyron repens	*Gnaphalium obtusifolium*
Antennaria sp.	*Lespedeza capitata*
Aster pilosus	*Linaria vulgaris*
Chrysanthemum leucanthemum	*Melilotus alba*
Equisetum arvense	*Monarda fistulosa*
Equisetum hyemale	*Ptelea trifoliata*
Erigeron strigosus	*Rudbeckia serotina*
Poa compressa	*Rumex acetosella*
Poa pratensis	*Solidago canadensis*
Potentilla recta	
Solidago juncea	
Solidago nemoralis	

The following is a list of the Orthoptera observed at Station 21A:

Acheta pennsylvanicus	*Melanoplus keeleri luridus*
Arphia p. pseudonietana	*Melanoplus s. scudderi*
Chorthippus longicornis	*Oecanthus exclamationis*
Dissosteira carolina	*Oecanthus n. nigricornis*
Encoptolophus s. sordidus	*Oecanthus n. quadripunctatus*
Melanoplus b. bilituratus	*Orphulella speciosa*
Melanoplus confusus	*Pseudopomala brachyptera*
Melanoplus dawsoni	*Spharagemon b. bolli*
Melanoplus f.-r. femur-rubrum	*Syrbula admirabilis*

Station 22B.—High, grassy banks of the creek, midway between the dam and the stone bridge, Loch Alpine, Ann Arbor area. This area was a pasture when the present study was begun, but it is now the site of a housing development. Grasses and forbs, particularly *Cirsium, Dactylis, Poa,* and *Taraxacum,* were abundant along these banks.

Station 25.—Marsh to the northwest of Cedar Bend Drive, Island Park, Ann Arbor. This seldom-inundated marsh, which is now the site of a housing development, is bordered by a well-traveled road and by higher, cleared ground. The station was formerly encircled by a narrow tree-shrub zone peripheral to a zone of sedges and grasses and a central zone of *Solidago* spp., and other forbs. The elevation is 760 feet and the soil Griffin loam.

The relative abundance of the more prominent plants of Station 25 is as follows:

Abundant

Agrostis alba
Aster lateriflorus
Eleocharis calva
Equisetum arvense
Juncus tenuis
Juncus torreyi
Leersia oryzoides
Solidago canadensis
Solidago graminifolia

Common

Acer negundo
Asclepias incarnata
Aster novae-angliae

Common (Cont.)

Carex retrorsa
Carex stricta var. *strictior*
Carex vulpinoidea
Daucus carota
Eupatorium perfoliatum
Eupatorium purpurem
Fraxinus americana
Lycopus americanus
Lysimachia ciliata
Mimulus ringens
Scirpus atrovirens
Scirpus validus
Tovara virginiana
Typha latifolia

The following is a list of the Orthoptera observed at Station 25:

Amblycorypha oblongifolia
Chorthippus longicornis
Conocephalus brevipennis
Conocephalus f. fasciatus
Melanoplus f.-r. femur-rubrum
Nemobius fasciatus
Neoconocephalus ensiger
Oecanthus n. nigricornis
Orchelimum gladiator
Orchelimum nigripes
Scudderia c. curvicauda
Scudderia texensis

Station 27.—Southwest Field, George Reserve. This dry field is an example of the mixed grass-herbaceous habitat of Cantrall (1943). It is surrounded by open woods and scattered trees. Its most elevated portion is a flat, westwardly directed ridge border-

ing on Southwest Woods. The crown of the ridge is dominated by *Aristida* and *Rubus*, while the shoulders are dominated by *Monarda* and *Poa compressa*. To the south it slopes down into a swale covered by considerable *Poa pratensis*. Its elevation ranges from 950 to 975 feet.

The relative abundance of the more prominent plants of Station 27 is as follows:

Abundant

Achillea millefolium
Aristida purpurascens
Monarda fistulosa
Oxalis stricta
Poa compressa
Rumex acetosella

Common

Antennaria plantaginifolia
Asclepias syriaca
Daucus carota

Common (Cont.)

Liatris aspera
Panicum oligosanthes
Poa pratensis
Potentilla recta
Rhus glabra
Rhus toxicodendron
Rubus flagellaris
Solidago juncea
Tragopogon pratensis
Hieracium longipilum

The following is a list of the Orthoptera observed at Station 27:

Acheta pennsylvanicus
Amblycorypha oblongifolia
Amblycorypha rotundifolia
Arphia p. pseudonietana
Arphia sulphurea
Atlanticus testaceus
Chloealtis conspersa
Chorthippus longicornis
Conocephalus strictus
Diapheromera femorata
Dissosteira carolina
Melanoplus b. bilituratus
Melanoplus bivittatus
Melanoplus confusus
Melanoplus f.-r. femur-rubrum
Melanoplus keeleri luridus
Nemobius allardi
Neoconocephalus ensiger
Neoconocephalus robustus crepitans
Oecanthus niveus
Oecanthus nigricornis quadripunctatus
Orchelimum sp.
Parcoblatta uhleriana
Parcoblatta virginica
Parcoblatta pensylvanica
Pardalophora apiculata

Orthoptera at Station 27 (cont'd.):

Pseudopomala brachyptera
Schistocerca lineata
Scudderia c. curvicauda
Spharagemon b. bolli
Spharagemon collare
Stethophyma gracile
Syrbula admirabilis

Station 28.—Colonel's Field, George Reserve. This field is another example of Cantrall's mixed grass-herbaceous habitat. Its rather flat surface is bounded by woods, scattered trees, and an unimproved main road. Its vegetation is largely *Aristida, Poa compressa, Solidago* spp., and various other herbs. Swales are not well-developed. The field-wood ecotone contains a few trees, scattered oak and other seedlings, tangled growths of *Rubus,* and various forbs and grasses, while its floor bears considerable leaf litter. This station is similar to Station 26.

Station 28B.—Blow-Out, George Reserve. The Blow-Out, an example of Cantrall's sparsely vegetated sand habitat, is a sandy dry field supporting a xeric association of plants. The northwestern part of the habitat is an area of shifting sands and little vegetation except mosses, lichens, and patches of *Cyperus* and *Panicum.* The remainder, however, is somewhat more generously covered with clumped *Aristida, Lespedeza, Panicum,* mosses, and lichens. The density of plant covering has notably increased since the habitat's description by Cantrall in 1943. The elevation of the Blow-Out ranges from 905 to 920 feet, and its soil is Bellefontaine sandy loam.

The relative abundance of the more prominent plants of Station 28B is as follows:

Abundant

Aristida purpurascens
Lespedeza capitata
Panicum spp.

Common

Asclepias syriaca

Common (Cont.)

Cyperus filiculmis
Erigeron strigosus
Poa compressa
Poa pratensis
Quercus velutina
Rumex acetosella

The following is a list of the Orthoptera observed at Station 28B:

Arphia p. pseudonietana
Dissosteira carolina
Encoptolophus s. sordidus
Melanoplus b. bilituratus
Melanoplus confusus
Melanoplus f.-r. femur-rubrum
Melanoplus s. scudderi
Schistocerca lineata
Spharagemon b. bolli
Spharagemon collare

Station 28C.—Field margin directly adjacent to the eastern end of Crane Pond, George Reserve. This bank is covered by *Asclepias, Cirsium,* grasses, and other herbs.

Station 28D.—Big Swamp, George Reserve. This marsh, an example of Cantrall's semipermanent marsh habitat, is choked by a dense growth of grasses, sedges, and forbs. The particular section visited in this study is a narrow band somewhat midway between the margin of Big Woods and Big Island. *Calamagrostis, Carex stricta* var. *strictior, Impatiens, Polygonum, Typha,* and ferns dominate the area. *Larix* is restricted to the center of the marsh, while *Rhus* is dispersed throughout it. The elevation is 895 feet and the soil Rifle peat.

The relative abundance of the more prominent plants of Station 28D is as follows:

Abundant

Calamagrostis canadensis
Carex lacustris
Carex stricta var. *strictior*
Carex spp.
Impatiens capensis
Onoclea sensibilis
Phalaris arundinacea
Polygonum sagittatum

Common

Betula pumila
Boehmeria cylindrica
Bromus sp.
Cicuta bulbifera

Common (Cont.)

Cornus stolonifera
Dryopteris thelypteris var. *pubescens*
Equisetum arvense
Eupatorium purpureum
Larix laricina
Populus tremuloides
Potentilla fruticosa
Rhus vernix
Scirpus spp.
Solanum dulcamara
Spiraea alba
Typha latifolia

The following is a list of the Orthoptera observed at Station 28D:

Amblycorypha oblongifolia
Chloealtis conspersa
Chorthippus longicornis
Conocephalus brevipennis
Conocephalus nigropleurum
Diapheromera femorata
Melanoplus bivittatus
Melanoplus f.-r. femur-rubrum
Neoconocephalus ensiger
Orchelimum gladiator
Orchelimum nigripes
Paroxya hoosieri
Pseudopomala brachyptera
Scudderia c. curvicauda
Scudderia f. furcata
Tetrix subulata
Tettigidea l. lateralis

Station 29.—Marsh immediately southeast of Geddes Bridge, Ann Arbor area. This habitat is the permanently marshy border of the Huron River. Its width varies from 10 to 50 feet from the river margin to the railroad embankment which overlooks it. It has three narrow zones: a shrub zone dominated by *Cornus* and contiguous with the railroad embankment; a central zone or marsh proper dominated by *Carex, Eupatorium* spp., and *Juncus;* an aquatic zone bordering the river and dominated by *Carex comosa* and *Peltandra.* The elevation is 740 feet and the soil Carlisle muck.

The relative abundance of the more prominent plants of Station 29 is as follows:

Abundant	Common
Agrostis alba	*Cornus stolonifera*
Bidens cernua	*Eupatorium perfoliatum*
Carex comosa	*Lycopus virginicus*
Eupatorium purpureum	*Sagittaria latifolia*
Impatiens capensis	*Scirpus validus*
Juncus effusus	*Verbena hastata*
Leersia oryzoides	
Peltandra virginica	

The following is a list of the Orthoptera observed at Station 29:

Acheta pennsylvanicus
Conocephalus attenuatus
Conocephalus f. fasciatus
Melanoplus bivittatus
Melanoplus f.-r. femur-rubrum
Orchelimum nigripes
Orchelimum volantum

Station 31.—Big Woods, George Reserve. This oak-hickory woods, the shady oak-hickory habitat of Cantrall, occurs on the crown and sides of a rather steep, extensive, esker-like ridge between Big Swamp and a series of depressions to its northwest. The top of the ridge is traversed by a well-traveled, unimproved road. The tall-tree stratum is of oaks and hickories, while the shrub stratum is largely of *Prunus,* though *Gaylussacia* is also very common. The ground stratum is mostly *Carex pensylvanica* and *Pteridium.* The forest floor is covered by an abundant leaf litter and considerable broken branches and twigs. The elevation of the habitat ranges from 900 to 975 feet, and its soil is Bellefontaine sandy loam.

The relative abundance of the more prominent plants of Station 31 is as follows:

Abundant	Common (Cont.)
Carex pensylvanica	*Carya ovata*
Prunus serotina	*Gaylussacia baccata*
Pteridium aquilinum var. *latiusculum*	*Hamamelis virginiana*
Quercus alba	*Hepatica americana*
Quercus velutina	*Poa compressa*
	Quercus rubra
Common	*Rubus flagellaris*
Carya glabra	*Sassafras albidum*

The following is a list of the Orthoptera observed at Station 31:

Acheta pennsylvanicus	*Oecanthus angustipennis*
Atlanticus testaceus	*Parcoblatta pensylvanica*
Ceuthophilus brevipes	*Parcoblatta uhleriana*
Ceuthophilus meridionalis	*Scudderia c. curvicauda*
Chloealtis conspersa	*Scudderia f. furcata*
Diapheromera femorata	*Scudderia septentrionalis*
Nemobius tinnulus	

Station 31B.—Northeast Field, George Reserve. This dry field, an example of Cantrall's mixed grass-herbaceous habitat, is somewhat concave in profile, the resulting variation in soil

moisture accounting for much of the interesting vegetational zonation. To the north there is a low ridge, the vegetation of which is mostly *Poa compressa* and *Rumex,* and to the south a gentle rise to the border of Big Woods, the vegetation of which is dominated by *Aristida, Rhus,* and *Solidago* spp. Nestled in the small concavity between the above ridges is an area of *Phleum* and *Poa pratensis,* together with small, localized patches of *Asclepias, Cirsium, Monarda,* and *Setaria.* The elevation of the habitat ranges from 910 to 925 feet, and its soil is Bellefontaine sandy loam.

The relative abundance of the more prominent plants of Station 31B is as follows:

Abundant

Aristida purpurascens
Asclepias syriaca
Cirsium arvense
Monarda fistulosa
Phleum pratense
Poa compressa
Poa pratensis
Rhus glabra
Rumex acetosella

Common

Achillea millefolium

Common (Cont.)

Antennaria spp.
Danthonia spicata
Daucus carota
Desmodium sessilifolium
Erigeron strigosus
Euphorbia corollata
Hieracium longipilum
Lespedeza capitata
Potentilla recta
Rubus flagellaris
Solidago juncea
Solidago nemoralis

The following is a list of the Orthoptera observed at Station 31B:

Acheta pennsylvanicus
Atlanticus testaceus
Camnula pellucida
Chloealtis conspersa
Conocephalus brevipennis
Conocephalus strictus
Dissosteira carolina
Encoptolophus s. sordidus
Melanoplus b. bilituratus
Melanoplus bivittatus
Melanoplus confusus
Melanoplus f.-r. femur-rubrum
Melanoplus keeleri luridus
Nemobius allardi
Neoconocephalus ensiger
Oecanthus nigricornis quadripunctatus
Schistocerca lineata
Scudderia c. curvicauda
Spharagemon b. bolli
Spharagemon collare
Syrbula admirabilis

Station 35.—John Bryan State Park, Ohio. Woodland trail.

Station 36.—Mohican State Park, Ohio. Woodland trail.

Station 37.—Mount Giliad State Park, Ohio. Woodland trail.

Station 38.—Old Man's Cave State Park, Ohio. Wood opening of half-coniferous, half-deciduous woodland. The conifers are largely *Tsuga.*

Station 39.—Stroud's Run State Park, Ohio. Dense woodland with considerable leaf litter.

Station 40.—Yard of house, 624 Packard Street, Ann Arbor. This is a small, partly shaded, grass-covered lawn fringed with cultivated plants, including forbs and shrubs.

APPENDIX C
PLANTS USED IN STUDY

The common and specific names of plants and the classification of plants adopted for this work are those of Fernald's *Gray's Manual of Botany* (1950). Those plants on which feeding was recorded in nature and those used in laboratory feeding tests are listed below.[36] This list includes 197 species belonging to 54 plant families. Virtually all of the determinations were made by the author by reference to standard works and comparison with identified materials in the Herbarium of the University of Michigan, but Dr. Rogers McVaugh and Mr. Jarl Hiltunen kindly assisted in the determination of a number of difficult specimens. Identifications made on vegetative characters alone, in groups where floral or other special features are required for accurate specific naming, were carried with assurance only to the genus or generic section, as the material would permit; the specific names given such plants are approximations. It will be noted that the species are numbered; for economy these code numbers are substituted for the plant names in the report on the differential feeding tests.

Division PTERIDOPHYTA

Family Equisetaceae (horsetails)

1. *Equisetum arvense* (common horsetail) [37]
2. *Equisetum hyemale* (scouring rush)

Family Polypodiaceae

3. *Onoclea sensibilis* (sensitive fern)
4. *Pteridium aquilinum* var. *latiusculum* (brake)

Division SPERMATOPHYTA

Subdivision GYMNOSPERMAE

Family Pinaceae (pines)

5. *Tsuga canadensis* (hemlock)

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[36] Plants simply observed in the habitats are named in the habitat descriptions, Appendix B, but are not listed here.

[37] The describer's name is not given but can be obtained by reference to Fernald (1950).

Subdivision ANGIOSPERMAE

Class MONOCOTYLEDONEAE

Family Typhaceae (cat-tails)

6. *Typha angustifolia*
7. *Typha latifolia* (common cat-tail)

Family Alismataceae (water-plantains)

8. *Alisma triviale* (water-plantain)
9. *Sagittaria latifolia* (wapato)

Family Graminiae (grasses)

10. *Agropyron repens* (witch-grass)
11. *Agrostis alba* (redtop)
12. *Andropogon gerardi* (beard-grass)
13. *Aristida purpurascens* (triple-awned grass)
14. *Bromus inermis*
15. *Calamagrostris canadensis* (blue-joint)
16. *Dactylis glomerata* (orchard-grass)
17. *Danthonia spicata* (poverty-grass)
18. *Digitaria sanguinalis* (crab-grass)
19. *Echinochloa crusgalli* (barnyard-grass)
20. *Elymus virginicus* (terrell grass)
21. *Eragrostis spectabilis* (tumble-grass)
22. *Leersia oryzoides* (rice-cutgrass)
23. *Muhlenbergia schreberi* (drop-seed)
24. *Panicum lanuginosum*
25. *Panicum* spp. (panic-grass)
26. *Phalaris arundinacea* (reed-canary-grass)
27. *Phleum pratense* (common timothy)
28. *Poa compressa* (Canada bluegrass)
29. *Poa pratensis* (Kentucky bluegrass)
30. *Setaria glauca* (foxtail)

Family Cyperaceae (sedges)

31. *Carex communis*
32. *Carex comosa*
33. *Carex pensylvanica*
34. *Carex retrorsa*
35. *Carex stricta* var. *strictior*
35.' *Carex tribuloides*
36. *Carex vulpinoidea*
37. *Cyperus filiculmis* (galingale)
38. *Eleocharis calva* (spike-rush)
39. *Scirpus atrovirens*
40. *Scirpus lineatus*
41. *Scirpus validus* (great bulrush)

Family Araceae (arums)

42. *Acorus calamus* (sweetflag)
43. *Peltandra virginica* (tuckahoe)

Family Juncaceae (rushes)

44. *Juncus effusus*
45. *Juncus tenuis*
46. *Juncus torreyi*

Family Liliaceae (lilies)

47. *Allium cernuum* (wild onion)
48. *Asparagus officinalis* (garden asparagus)
49. *Convallaria majalis* (lily-of-the-valley)
50. *Smilacina racemosa* (false spikenard)
51. *Smilax herbacea* (carrion-flower)
52. *Smilax rotundifolia* (common greenbrier)

Family Iridaceae (irises)

53. *Sisyrinchium angustifolium* (blue-eyed grass)

Class DICOTYLEDONEAE

Family Salicaceae (willows)
54. *Populus deltoides* (cottonwood)
55. *Populus tremuloides* (quaking aspen)
56. *Salix* spp. (willows)

Family Juglandaceae (walnuts)
57. *Carya glabra* (pignut)
58. *Carya ovata* (shagbark-hickory)

Family Corylaceae (hazels)
59. *Betula pumila* (swamp-birch)
60. *Carpinus caroliniana* (blue beech)
61. *Corylus americana* (American hazelnut)

Family Fagaceae (beeches)
62. *Fagus grandifolia* (beech)
63. *Quercus alba* (white oak)
64. *Quercus bicolor* (swamp-white oak)
65. *Quercus macrocarpa* (mossy-cup oak)
66. *Quercus rubra* (red oak)
67. *Quercus velutina* (black oak)

Family Ulmaceae (elms)
68. *Ulmus rubra* (slippery elm)

Family Polygonaceae (buckwheats)
69. *Polygonum sagittatum* (arrow-leaved tearthumb)
70. *Rumex acetosella* (sheep-sorrel)
71. *Rumex crispus* (yellow dock)
72. *Tovara virginiana* (jump-seed)

Family Caryophyllaceae (pinks)
73. *Lychnis alba* (white cockle)

Family Ranunculaceae (crowfoots)
74. *Anemone virginiana* (thimbleweed)
75. *Anemonella thalictroides* (rue-anemone)

Family Berberidaceae (barberries)
76. *Podophyllum peltatum* (wild jalap)

Family Lauraceae (laurels)
77. *Sassafras albidum* (white sassafras)

Family Cruciferae (mustards)
77.′ *Berteroa incana*
78. *Brassica nigra* (black mustard)

Family Hamamelidaceae (witch-hazels)
79. *Hamamelis virginiana* (witch-hazel)

Family Rosaceae (roses)
80. *Crataegus* spp. (hawthorns)
81. *Fragaria virginiana* (strawberry)
82. *Potentilla fruticosa* (shrubby cinquefoil)
82.′ *Potentilla intermedia*
83. *Potentilla recta*
84. *Prunus serotina* (black cherry)
85. *Rubus flagellaris*
86. *Rubus occidentalis* (black raspberry)
87. *Spiraea alba* (meadow-sweet)

Family Leguminosae (pulses)
88. *Coronilla varia* (crown-vetch)
89. *Desmodium canadense* (beggar's-tick)
90. *Desmodium glutinosum*
91. *Desmodium illinoense*
91.′ *Desmodium paniculatum*
92. *Desmodium sessilifolium*
93. *Lespedeza capitata* (bush-clover)
94. *Lespedeza hirta*
95. *Medicago lupulina* (black medick)
96. *Melilotus alba* (white melilot)
97. *Melilotus officinalis* (yellow melilot)
98. *Trifolium hybridum* (alsike clover)

99. *Trifolium pratense* (red clover)
100. *Trifolium repens* (white clover)

FAMILY OXALIDACEAE (wood-sorrels)
101. *Oxalis stricta* (wood-sorrel)

FAMILY RUTACEAE (rues)
102. *Ptelea trifoliata* (wafer-ash)

FAMILY EUPHORBIACEAE (spurges)
103. *Euphorbia corollata* (flowering spurge)

FAMILY ANACARDIACEAE (cashews)
104. *Rhus glabra* (smooth sumac)

FAMILY STAPHYLEACEAE (bladdernuts)
105. *Staphylea trifolia* (bladdernut)

FAMILY ACERACEAE (maples)
106. *Acer negundo* (box-elder)
107. *Acer rubrum* (red maple)

FAMILY BALSAMINACEAE (touch-me-nots)
108. *Impatiens capensis* (spotted touch-me-not)

FAMILY RHAMNACEAE (buckthorns)
109. *Rhamnus alnifolia* (buckthorn)

FAMILY VITACEAE (vines)
110. *Parthenocissus quinquefolia* (Virginia creeper)
111. *Vitis riparia* (frost-grape)

FAMILY TILIACEAE (lindens)
112. *Tilia americana* (basswood)

FAMILY GUTTIFERAE (St. John's-worts)
113. *Hypericum perforatum* (common St. John's-wort)

FAMILY VIOLACEAE (violets)
114. *Viola papilionacea* (violet)

FAMILY ONAGRACEAE (evening-primroses)
115. *Oenothera biennis* (evening-primrose)

FAMILY UMBELLIFERAE (parsleys)
116. *Cicuta maculata* (spotted cowbane)
117. *Daucus carota* (Queen Anne's-lace)

FAMILY CORNACEAE (dogwoods)
118. *Cornus florida* (flowering dogwood)
118.′ *Cornus racemosa*
119. *Cornus stolonifera* (red osier)

FAMILY ERICACEAE (heaths)
120. *Gaylussacia baccata* (black huckleberry)

FAMILY PRIMULACEAE (primroses)
121. *Lysimachia ciliata* (loosestrife)

FAMILY OLEACEAE (olives)
122. *Fraxinus americana* (white ash)
123. *Syringa vulgaris* (common lilac)

FAMILY APOCYNACEAE
123.′ *Apocynum androsaemifolium*

FAMILY ASCLEPIADACEAE (milkweeds)
124. *Asclepias incarnata* (swamp-milkweed)
125. *Asclepias syriaca* (common milkweed)
125.′ *Asclepias tuberosa* (butterfly weed)

FAMILY VERBENACEAE (vervains)
126. *Verbena hastata* (blue vervain)
127. *Verbena urticifolia* (white vervain)

FAMILY LABIATAE (mints)
128. *Collinsonia canadensis* (richweed)
129. *Glechoma hederacea* (gill-over-the-ground)
130. *Lycopus americanus* (water-horehound)
131. *Lycopus virginicus*
132. *Mentha arvensis*
133. *Mentha piperita* (peppermint)
134. *Monarda fistulosa* (wild bergamot)
135. *Prunella vulgaris* (heal-all)

FAMILY SOLANACEAE (nightshades)
136. *Solanum dulcamara* (bitter-sweet)
FAMILY SCROPHULARIACEAE (figworts)
137. *Gerardia pedicularia* (gerardia)
138. *Linaria vulgaris* (butter-and-eggs)
139. *Mimulus ringens* (monkey-flower)
139.' *Penstemon hirsutus*
140. *Verbascum thapsus* (common mullein)
141. *Veronicastrum virginicum* (Culver's-root)
FAMILY PLANTAGINACEAE (plantains)
142. *Plantago lanceolata* (ribgrass)
143. *Plantago major* (common plantain)
144. *Plantago rugelii*
FAMILY RUBIACEAE (madders)
145. *Galium concinnum* (bedstraw)
FAMILY CAPRIFOLIACEAE (honeysuckles)
146. *Lonicera tatarica* (Tartarian honeysuckle)
FAMILY CAMPANULACEAE (bluebells)
147. *Campanula rotundifolia* (bluebell)
FAMILY COMPOSITAE (composites)
148. *Achillea millefolium* (common yarrow)
149. *Ambrosia artemisiifolia* (common ragweed)
150. *Ambrosia trifida* (great ragweed)
151. *Antennaria fallax* (pussy's-toes)
152. *Aster cordifolius*
153. *Aster laevis*
154. *Aster lateriflorus*
155. *Aster macrophyllus*
156. *Aster novae-angliae* (New England aster)
157. *Aster pilosus*
158. *Aster puniceus*
159. *Aster sagittifolius*
160. *Bidens coronata* var. *trichosperma* (bur-marigold)
161. *Cacalia atriplicifolia* (pale Indian-plantain)
162. *Chrysanthemum leucanthemum* (white daisy)
163. *Cichorium intybus* (common chicory)
164. *Cirsium arvense* (Canada thistle)
164.' *Cirsium vulgare*
164.'' *Erechtites hieracifolia*
164.''' *Erigeron canadensis*
165. *Erigeron strigosus* (daisy-fleabane)
166. *Eupatorium perfoliatum* (thoroughwort)
167. *Eupatorium purpureum* (sweet joe-pyeweed)
168. *Gnaphalium obtusifolium* (catfoot)
169. *Helianthus divaricatus* (sunflower)
170. *Hieracium longipilum* (hawkweed)
171. *Lactuca biennis* (lettuce)
171.' *Lactuca canadensis*
172. *Liatris aspera* (button-snakeroot)
173. *Polymnia canadensis* (leafcup)
174. *Rudbeckia serotina* (coneflower)
175. *Solidago caesia* (blue-stem goldenrod)
176. *Solidago canadensis*
177. *Solidago graminifolia*
178. *Solidago juncea*
179. *Solidago nemoralis*
180. *Solidago rigida*
180.' *Solidago speciosa*
181. *Sonchus arvensis* (field sow-thistle)

182. *Taraxacum officinale* (common dandelion)
183. *Tragopogon pratensis* (goat's-beard)
184. *Vernonia altissima* (ironweed)

THE ALTITUDINAL DISTRIBUTION OF MOSQUITO LARVAE IN THE COLORADO FRONT RANGE [1]

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In the abundant literature concerning the ecology of mosquitoes, little attention has been directed toward the relationships between altitude and species habitats in mountainous regions. The present study was undertaken in an effort to determine altitudinal and ecological relationships of mosquitoes in a representative portion of the Colorado Front Range, the easternmost cordillera of the Rocky Mountains. Boulder County was chosen for the study because it presents a wide altitudinal range in a relatively compact and well-defined geographical area. The eastern half of the county is the westernmost extension of the Great Plains, and slopes very gradually from 4900 to 6000 feet in altitude. The western half of the county rises abruptly as the Colorado Front Range approaches the Continental Divide, which is found at the 12,000 to 13,500 foot level, and which forms the western boundary of the county. A wide variety of mosquito larval habitats is afforded in such an area, altitudinally as well as ecologically. Latitudinal limits of the county are 39° 55′ and 40° 15′ N.

Only the mosquito larval forms were treated in this investigation for two reasons. The first consideration was to relate the species altitudinally, and this was better done by using actual oviposition sites as criteria of the species' natural altitudinal distribution. Secondly, use of larval specimens only excludes any adult members of species that may have migrated into the study area from adjoining regions.

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Collections of larvae were made throughout the summer and fall months of 1959 and 1960, and, in the plains region, in the winter months also. It was possible to do all collecting by means of a long-handled aquatic dipnet. The specimens were transferred to vials containing 80% ethyl alcohol, and taxonomic determinations were made in the laboratory. Since this study is primarily of a qualitative nature, no attempt was made to obtain quantitative data. Altitudinal determinations were made by means of topographic maps published by the United States Department of the Interior.

Description of Habitats

For clarity, and to aid in the description of typical habitats, the altitudinal regions have been grouped as follows:

Plains region	4,900– 6,000 ft.
Foothills region	6,000– 8,000 ft.
Montane region	8,000–10,000 ft.
Alpine region	10,000–12,000 ft.

Frequently, both subalpine and alpine zones are recognized in the altitudinal region from 10,000 to 12,000 feet. However, for purposes of this study, fauna of these altitudes will be grouped together, and designated alpine. The Continental Divide is the western boundary of the area, and no specimens were collected in the relatively small and precipitous area of mountain peaks between this boundary and the 12,000-foot contour.

Plains Region.—The eastern one-third of Boulder County lies principally between the 5000- and 6000-foot altitudinal contours, and habitats of this area are treated as those typical of the plains region. These habitats result largely from man's influence, as nearly all sizable bodies of water are the result of damming natural drainages, or are artificial reservoirs. Seepage areas from irrigation ditches and reservoirs, and drainage areas from roads constitute the great majority of larval habitats in this region. Household containers are seldom found as mosquito habitats in Colorado's dry climate, since the water in small containers usually evaporates before the egg-larval cycle can be completed.

Foothills Region.—The land between the 6000- and 8000-foot contours is a region where water is found mainly in turbulent mountain creeks. The rapid descent of these streams provides no appropriate breeding places for mosquitoes, and except in the early spring, very few standing pools of water are to be found in the foothills.

Montane Region.—The montane region, lying between 8000 and 10,000 feet, is a zone of broad mountain valleys interspersed with ridges extending eastward from the Continental Divide. Mosquito larval habitats are abundant during spring and early summer as the melting snow collects in hollows in the still-frozen ground. The valley meadows become saturated and fill with numerous pools of standing water. Large areas along the roadsides are inundated, and many of the numerous brooks of the region overflow their banks. In addition, there are a number of ponds of a more permanent nature with a varied flora and fauna.

Alpine Region.—The alpine region has abundant locations suitable for the development of mosquito larvae. Those of the alpine tundra are relatively consistent in nature, being mostly rocky "tarns" formed on solifluction terraces as the result of slow movement of soil over a solid underlying base, in this case permanently-frozen ground. Some of the alpine habitats are located well below timberline, and among the most common of these are the strings of rock basin or "paternoster" lakes. The shallow edges of these lakes and the many spring overflow pools surrounding them make ideal sites for mosquito development, and during the spring and early summer months, these sites are by far the most prolific for mosquito production in the study area.

Notes on the Species

This study resulted in the discovery in Boulder County of 18 of the 45 species previously reported for the state of Colorado (Cockerell, 1918; Dyar, 1922, 1924; Matheson, 1933, 1944; James, 1942; Portman, 1943; Olson and Keegan, 1944a, 1944b; Laskey, 1946; Harmston, 1949; Thompson *et al.*, 1951), and three species not heretofore recorded for this state. These include:

Aedes campestris Dyar and Knab
A. cataphylla Dyar
A. communis (DeGeer)
A. dorsalis (Meigen)
A. fitchii (Felt and Young)
A. hexodontus Dyar
A. impiger (Walker)
A. implicatus Vockeroth
A. melanimon Dyar
A. pionips Dyar
A. pullatus (Coquillett)
A. punctor (Kirby)
A. schizopinax Dyar
Aedes trivittatus (Coquillett)
A. vexans (Meigen)
Culex pipiens Linnaeus
C. tarsalis Coquillett
C. territans Walker
Culiseta impatiens (Walker)
C. incidens (Thompson)
C. inornata (Williston)

Of the species found, *A. pionips* has been reported only once (Dyar, 1924), and not subsequently substantiated by other investigators. In addition, *A. punctor,* recorded by Dyar (1924) and Harmston (1949), was later reidentified as *A. hexodontus* (Knight, 1951). Specimens of all three of these species were collected in the present study, as well as *Culex territans* and *Aedes schizopinax,* which have not been reported previously in Colorado. *Aedes impiger* (recorded as *Aedes nearcticus,* see Vockeroth, 1954) has been represented in Colorado records by a single adult male taken by Matheson (1944) at Alamosa, Colorado.

Aedes (Ochlerotatus) campestris Dyar and Knab

This species was collected in a single location, in overflow pools lying at the edge of a plains lake (5185 ft.). These well-illuminated pools have silty bottoms, with almost no organic deposits, little vegetation, and an appearance of alkalinity evidenced by dried peripheral whitish rings. The water is colored, rich in organic materials, and from six to ten inches deep. These fourth-instar larvae were collected on November 9 and November 21, 1959, following a period of sub-freezing temperatures, in water of 3° and 4°, and under a three-eighths to one-inch layer of ice. Previous collections at the same location in August, September, and October revealed only *A. dorsalis* and some *Culex tarsalis.*

Aedes (Ochlerotatus) cataphylla Dyar

Specimens of *A. cataphylla* were collected at altitudes ranging from 8450 to 10,350 feet, from late May through July. The larval habitats varied from a small pool less than a square meter in

Table 1.—The altitudinal distribution of Front Range mosquito larvae.

Plains Region (4900–6000 ft.)

Aedes campestris	*A. trivittatus*	*C. tarsalis*
A. dorsalis	*A. vexans*	*C. territans*
A. melanimon	*Culex pipiens*	*Culiseta inornata*

Foothills Region (6000–8000 ft.)

Aedes schizopinax	*Culiseta impatiens*	*C. inornata*
Culex tarsalis		

Montane Region (8000–10,000 ft.)

Aedes cataphylla	*A. implicatus*	*Culiseta impatiens*
A. communis	*A. pionips*	*C. incidens*
A. fitchii	*A. pullatus*	*C. inornata*
A. hexodontus	*A. punctor*	

Alpine Region (10,000–12,000 ft.)

Aedes cataphylla	*A. impiger*	*A. punctor*
A. communis	*A. pionips*	*Culiseta impatiens*
A. fitchii	*A. pullatus*	*C. incidens*
A. hexodontus		

size, a few centimeters deep, and almost completely covered with an algal mat, to large, shallow, open, roadside pools with little vegetation other than trees. All of the pools where this species was found appeared to be formed as a result of melting snow, and three of the seven collection sites were located at the base of snowbanks. Three of the sites had thick vegetation of algae and grasses; four had little or no vegetation. Associated species were *A. pullatus, A. hexodontus, A. communis, A. fitchii,* and *A. pionips.*

Aedes (Ochlerotatus) communis (DeGeer)

Fourth-instar larvae of this species were collected at altitudes of 9750 to 10,300 feet, from the end of June until late August. The habitats were consistently swampy, shallow, and with abundant vegetation in and around the pools. They were also found within a comparatively small geographical area, all sites being within four square miles. This species was found in association with *A. hexodontus, A. pionips, A. pullatus,* and *A. cataphylla.*

Aedes (Ochlerotatus) dorsalis (Meigen)

Although the larvae of *Aedes dorsalis* were not found in a great number of locations, they were extremely abundant where found. Their distribution is entirely within the lower altitudinal portion of the plains zone (4900–5270 ft.), and the larvae were found mainly in semi-permanent bodies of water. There was usually vegetation present, and the water in many of the locations appeared rich in organic matter. *A. dorsalis* was found in association with *Culiseta inornata* and *Culex tarsalis* in most instances, but was associated in some habitats with *A. campestris, A. vexans, A. trivittatus*, and *A. melanimon.*

In one habitat, fourth-instar larvae of *A. dorsalis, Culex tarsalis, Culiseta inornata*, or a combination of the three were found in every month of the year except February and March. In March, 1960, this habitat contained many first and second instar larvae, making February the only month when no mosquito larvae were present. During the winter months, there was often a one to two-inch ice covering over the entire water surface, broken only by the grassy vegetation. This location, near the eastern edge of the county at an altitude of 4950 ft., appears to be a remnant of an oxbow lake near the point where Boulder Creek crosses into Weld County. The site has some water in it throughout the year, although it becomes very low during the hot summer months. It is alkali-encrusted around the sides, and has abundant vegetation of the grass-sedge-rooted-emergent complex.

Aedes (Ochlerotatus) fitchii (Felt and Young)

Aedes fitchii larvae were found in only two locations, one at 8650 feet, and the other at 10,350 feet. Both locations were shallow bodies of water with little vegetation. The one at the higher elevation was run-off water from melting snow; the other was apparently a more permanent pool which seems to persist throughout the year, except in periods of extreme dryness.

Aedes (Ochlerotatus) hexodontus Dyar

Larvae of this species were common at the higher altitudes, especially near and just above the 10,000-foot level. Total altitudinal range was 9200 to 11,600 feet, with only three of the 22 habitats below 9900 feet. *Aedes hexodontus* was found most

often in association with *A. pullatus*, and was also found with *A. cataphylla, A. punctor, A. pionips, A. communis,* and *A. impiger.* The habitats were varied in size, vegetation, and illumination, and often contained a considerable quantity of decaying vegetation. Fourth-instar larvae were collected from late June through August.

Aedes (Ochlerotatus) impiger (Walker)

Aedes impiger was collected from late June to mid-July in four locations at altitudes from 10,500 to 11,615 feet. All sites were shallow pools formed by melting snow and with little or no vegetation. These sites were not widespread, but were within a geographical area of about two square miles.

Aedes (Ochlerotatus) implicatus Vockeroth

This species was collected in a single location, at 8275 feet, in the grassy pools of the spring overflow of a mountain brook. It is a single brooded species that usually hatches early in the spring. These specimens were collected in early June. It is not a common species of the Rocky Mountain region.

Aedes (Ochlerotatus) melanimon Dyar

Aedes melanimon closely resembles *A. dorsalis,* and these two common plains species have undoubtedly been confused to some extent in previous records. In the present study, fourth-instar larvae were collected in two plains locations, both fed by irrigation overflow. Collections were made in early June and late August. Associated larvae were *A. vexans, A. dorsalis, A. trivittatus, Culex tarsalis,* and *Culiseta inornata.*

Aedes (Ochlerotatus) pionips Dyar

This species was found in three locations at elevations from 9500 to 10,300 feet, in association with *A. punctor, A. hexodontus, A. pullatus, A. communis,* and *A. cataphylla.* The habitats were small pools, six to 12 inches deep, surrounded by vegetation, but with little vegetation within the pool. These locations also supported abundant populations of aedine larvae of other species. Collections were made in June, July, and August, and each time many larvae were present, with at least three different species represented.

Aedes (Ochlerotatus) pullatus (Coquillett)

Aedes pullatus is by far the most ubiquitous and abundant species collected during this study. It was found in 58 locations ranging from 8275 to 11,700 feet in altitude, and except for *A. impiger,* is the only species to be found consistently at altitudes above 11,000 feet. Larvae were collected from late May through early August. The great variety and number of habitats where this species is found discourage detailed description. Suffice it to say that almost any water-filled depression seems to provide the ecological necessities for oviposition by the adult female, and that the larvae thrive in many habitats such as the rocky tarns of the alpine tundra where other species do not seem to be able to survive. Larval associates of *A. pullatus* were *A. cataphylla, A. communis, A. hexodontus, A. pionips, A. punctor, A. impiger, Culiseta impatiens,* and *C. inornata.*

Aedes (Ochlerotatus) punctor (Kirby)

Aedes punctor was found in four locations, ranging from 9500 to 11,200 feet in altitude. The larvae were collected between June 19 and July 14 from sites that appeared to be generally deeper and more permanent than many of the other alpine larval habitats. This species was found in association with *A. hexodontus, A. pionips, A. pullatus,* and *Culiseta impatiens.*

Aedes (Ochlerotatus) schizopinax Dyar

This rare species has previously been reported only in Montana and Mammoth Hot Springs, Wyoming (Mail, 1934) and in Utah (Rees and Nielsen, 1955). Larvae of this species were collected in early June, in a mountain pasture (7250 ft.) still inundated by melting snow. Few larvae were present in the location.

Aedes (Ochlerotatus) trivittatus (Coquillett)

Aedes trivittatus was collected in two locations at lower elevations in the plains region (5080 and 5110 ft.) in the latter part of July and August. One site was a roadside culvert with emergent vegetation, clear but colored water, and about 14 inches deep. Many associated larvae were present, including *A. dorsalis, A. vexans, Culex tarsalis* and *Culiseta inornata.* The other

location was a large, very shallow seepage area near an irrigation ditch. It contained some vegetation, mostly grasses. Associated larvae in this location were *A. vexans* and *A. melanimon.*

Aedes (Aedimorphus) vexans (Meigen)

Aedes vexans appears to be more common in the plains region than the collections in this study indicate. This species was taken in eight locales between 4900 and 5350 feet during the period from early June to early September. Most of the habitats were shallow, grassy, and temporary. Several collection sites were roadside culverts and drainages, and one consisted of overflow pools along Boulder Creek. This species was found in association with *A. trivittatus, A. dorsalis, A. melanimon, Culex tarsalis* and *Culiseta inornata.*

Culex (Culex) pipiens Linnaeus

Culex pipiens does not appear to be common in this area, and was collected in a single plains location (5236 feet), the trickle of a small spring brook flowing through a meadow. The larvae were found in late September; a month earlier *C. tarsalis* was collected in the same location.

Culex (Culex) tarsalis Coquillett

Culex tarsalis is the most common of the plains species, with a distribution that ranges from 4900 to 6200 feet altitudinally. When it was found in association with other larvae, it was usually with *Aedes dorsalis* and *Culiseta inornata*, often in what were essentially year-round habitats. However, in such places the *C. tarsalis* larvae were present only from April through October. This species was also associated at times with *A. vexans,* but most commonly it was the solitary species of a particular locale. Habitats were varied. Many were roadside drainages; seepage pools around the edges of reservoirs were common sites; spring pools, a stock tank, and stream overflow were also representative habitats.

Culex (Neoculex) territans Walker

This species was found in only one area, in the northern plains region of Boulder County (5160 ft.), in early September. Its habitat was the grassy edge of an irrigation reservoir, a relatively

unusual location. Mosquito larvae are more often found in pools along the edges, but separated from the reservoir proper, because of the many predators which usually occupy the main body of water.

Culiseta (Culiseta) impatiens (Walker)

Habitats of *Culiseta impatiens* ranged from 6500 to 10,400 feet in this study area, and this wide range is in keeping with the fact that *Culiseta* generally has a greater altitudinal spread than *Aedes* or *Culex*. Fourth-instar larvae were collected from late June to early September. Habitats were varied, but the majority of them were shaded, semi-permanent to permanent, with little vegetation, but with abundant seston in the water. Members of this genus seem to be more able to withstand a slight current in the larval habitat, perhaps thus accounting for their wider range. This species was associated with *C. incidens, Aedes pullatus,* and *A. punctor,* but was more often found alone.

Culiseta (Culiseta) incidens (Thompson)

Culiseta incidens was the least common of the three species of *Culiseta* found in the area. It was found in only five locations, but had a wide altitudinal range, from 6450 to 10,400 feet. It was collected from early June to early September. Habitats varied from very temporary snow-melt drainage in the lower foothills to relatively permanent pools in an alpine bog. In general, locations had low illumination and appeared rich in organic material. The larvae were found in association only with *C. impatiens.*

Culiseta (Culiseta) inornata (Williston)

This species was found to have the widest altitudinal range of the mosquitoes in Boulder County, from 4950 to 9900 feet. It was collected from May through the following January, at times under ice one to two inches thick, and was usually in association with *Culex tarsalis.* It was also found with *A. dorsalis, A. vexans,* and *A. pullatus.* It appears to be consistently present throughout the summer and fall months in this area. The habitats in which this species was found were generally permanent or semi-permanent, with abundant vegetation and much organic debris.

Ecological Discussion

In the literature dealing with mosquito ecology, many attempts have been made to categorize larval habitats into distinct classes. In this study, the tremendous diversity of larval habitats leads the present author to hesitate trying to so group them, for there were more exceptions than generalizations of the habitat types. Rather, it seems more profitable to examine limiting factors that may influence the species distribution.

Physical Factors

Temperature.—Surface water temperatures were taken at each collection site in this investigation. Little correlation was shown of temperature with distribution, except in the case of the high alpine species, *A. impiger,* and to a lesser extent, *A. hexodontus* and *A. punctor,* which seem to be found only in relatively cold water. Although there is undoubtedly a limiting factor of high temperature for mosquito larvae, this is rarely, if ever, met in the natural aquatic habitat, where temperature variation is much less than the changeable air temperature. The plains species appear able to adapt to relatively warm water (maximum in this study, 33° C.), and yet several of these species were also found surviving under one or two inches of ice in water at 3 to 4°.

Temperature does affect rate of development, however, and this is correlated very well with altitude. In one montane habitat where an essentially pure culture of *A. pullatus* larvae was found, first- and second-instar larvae were observed on June 19. Weekly observations of this spring-fed roadside pool, where the temperature was between 13 and 15° most of the time, showed slow but steady development, with second- and third-instar larvae in evidence on July 1, some fourth-instars present July 10, and the first pupae appearing July 17. By August 4, only a few pupae were left in this habitat. This period of larval development lasting from six to eight weeks was also seen in the alpine tundra. It contrasts greatly with the rapid cycle of some of the plains species, and could indeed be a limiting factor if the larval habitat were to dry up during this period.

Light.—The amount of light available to the mosquito larvae was seen to be an influence in several situations. Members of the genus *Culiseta* were found in the present investigation to be the most susceptible to light factors, and *Culiseta impatiens* and *C. incidens* were almost invariably found in a shaded area. *C. inornata* does not seem to have such specific light requirements, nor do the aedine and *Culex* species.

Surface.—Surface conditions of the aquatic habitats of mosquito larvae are of vital importance because of the necessity for the larvae to obtain atmospheric oxygen by means of the respiratory siphon. The present study failed to reveal any habitats where mosquito larvae survived when the surface was completely covered by even a thin layer of vegetation, fine silt, or debris.

This method of respiration also eliminates areas of moving water as larval habitats, presumably because of turbulence. Although some species are almost invariably found near lotic environments, the actual larval habitat is always a sheltered spot where movement of the water surface is slight or absent. This factor takes on added importance in areas of extensive irrigation. When water is kept running, there is little opportunity for a mosquito nuisance to develop.

Depth.—The only species in this study which appeared to be limited in any sense by the depth of water in the larval habitat was *A. punctor.* This species was found only in deeper (one to two feet) pools of the high altitudes. Whether this occurrence was controlled only by depth is uncertain. It may also have been a factor of permanancy or temperature.

Chemical Factors

Hydrogen-ion concentration, dissolved gases, and *organic content.*—Only occasionally in this study did these factors seem to have significance. Two of the plains habitats contained mosquito larvae until a much later date than any of the other locations. The author believes this resulted partly from the combination of pH (alkaline in both cases), inorganic salts, and in one case, organic content of the water.

Inorganic salts.—Mosquitoes of the inland regions do not usually have extensive adaptive mechanisms for salinity toleration. However, some of them do possess a limited degree of tolerance to concentrations of inorganic salts. This investigation indicated *A. dorsalis*, *C. tarsalis*, and *C. inornata* as the species possessing such tolerance in this geographical area.

Biological Factors

Microbiota.—Mosquito larvae are dependent on microscopic plants, animals, and detritus for food. Plankton organisms did not appear in these observations to have any limiting effect on mosquito larvae, except in the case of an algal scum that completely covered th surface area. In the alpine tundra, where plankton organisms are scarce, the larvae were seen to "browse" on the algal flora attached to the rock surfaces.

Vegetation.—Mosquito larval habitats have often been correlated with vegetation. However, in most cases the larval-floral association is not clear-cut, and reflects only a local situation. Also, the ecological succession of plants in a particular larval habitat may result in considerable changes in the vegetation over a period of years, without any change in the mosquito species which inhabit the locale.

The type of plant, rather than the species, is the influential factor in the association of mosquitos with the vegetation. Overhanging shrubs, shading a location, may make a considerable difference in the mosquitoes that breed and oviposit in that location. The species forming an algal mat is not as important as the fact that the mat is there. Although many of the locations in this study area had considerable vegetation in and around the water, it was not seen as a limiting factor in any location except where vegetation covered the water surface or affected the illumination of the pool.

Predators.—Predation of mosquito larvae by other animals is probably the greatest limiting factor in this area. Observations in the field soon made it obvious that mosquito larvae were not to be found in locations where fish, amphibians, many Coleoptera, or Hemiptera were present. In a few instances, mosquito larvae were collected in habitats where small tadpoles of

Bufo or *Rana* were present. Possibly, in these cases, the tadpoles were still young enough to be getting some nourishment from the yolk.

The predaceous insects most frequently observed were Dytiscidae and Notonectidae. Although the Gerridae are also supposedly predaceous, mosquito larvae were found in a number of locations where members of this group were present. Possibly an abundance of other food lowered the predation rate in these instances.

Interspecific competition. One of the interesting observations of this study was that many of the alpine habitats were occupied by several species of the genus *Aedes* at one time. This is contrary to Gause's principle that more than one species of a single genus cannot occupy a given ecological niche. A possible explanation of this phenomenon lies in the temporary nature of the larval occupation. However, as was noted previously, the larval developmental cycle at these altitudes often lasts for a period of two months. In addition, there are new larvae hatching every time the water level changes enough to allow the edges to become thoroughly dry, maintaining the population density over a period of as much as four months.

Seasonal cycles.—The single-broodedness of the mountain aedine species makes it somewhat difficult to follow seasonal incidence of these mosquitoes unless a single habitat proves suitable for a variety of species, thus providing a certain amount of successional data. Only two such well-defined associations were discovered in the higher altitudes of this area. A montane habitat (9500 ft.) in May had an association of *A. hexodontus* and *A. punctor,* and in June had *A. punctor, A. pullatus, A. hexodontus,* and *A. pionips* in association. In August, this habitat was occupied by *Culiseta impatiens.* In the alpine region (10,300 ft.) an association of *A. communis, A. hexodontus,* and *A. cataphylla* was collected near the end of July; this was followed three weeks later by an *A. hexodontus, A. pullatus, A. communis,* and *A. pionips* association. While these data are insufficient to give a complete picture of the seasonal mosquito cycle in the Colorado mountains, they do give an indication of *A. punctor* and *A. cataphylla* as early species, followed by *A. hexodontus* and *A.*

communis, and finally *A. pullatus* and *A. pionips. A. fitchii* probably occurs with the middle group, and *A. impiger* was collected only in mid-July. More data are needed, however, to define this cycle more clearly.

In the plains region, the ubiquitous *A. dorsalis-C. tarsalis-C. inornata* association is present through most of the year, while *A. vexans* makes its appearance only in the summer months. The other plains species were collected in too few numbers to draw any conclusions as to their annual cycles.

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A SYNOPSIS OF THE CARPENTER BEES BELONGING TO THE SUBGENUS XYLOCOPOIDES MICHENER (HYMENOPTERA; APOIDEA)

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The chiefly Nearctic subgenus *Xylocopoides* Michener (1954: 155), as restricted by Hurd (1956), is composed of several medium-sized species of the genus *Xylocopa* which usually exhibit a brightly metallic bluish, greenish, or purplish integument. Consequently these species are superficially similar in appearance to certain species belonging to the essentially Neotropical subgenus *Schönherria* Lepeletier. Structurally, however, the subgenus *Xylocopoides* occupies an isolated position among the New World *Xylocopa*, apparently having been derived from the ancestors of the Old World *Xylocopa* proper (Hurd, 1956: 4). The males differ markedly from other New World groups of *Xylocopa* by the thick, apically truncated gonocoxites and by the uniquely hirsute penis valves (plate VII, figs. 1–4). The females possess a complex pygidial area (plate VIII, fig. 7) which is not shared by other subgenera of the genus *Xylocopa*. The pygidial plate is armed, as in many other *Xylocopa*, on each side with a subapical spine which, unlike other *Xylocopa*, are each preceded anteriorly by a diverging row of spine-like teeth, the prepygidial denticles. The deeply foveate basitibial plates (plate VIII, fig. 9) are also an unusual feature of the females included in the subgenus *Xylocopoides*.

This report was undertaken primarily so as to provide keys for the identification of the species and subspecies comprising the subgenus *Xylocopoides*. Although I have previously treated two of these species (Hurd, 1955), the Mexican representatives (one described here as new) have remained almost unknown since their original descriptions. The key to the subspecies of *Xylocopa virginica* (Linnaeus) presented in my earlier study (Hurd, 1955: 50) has been modified so as to include a new subspecies from southern Florida. This subspecies was recently called to my attention by Dr. Karl V. Krombein who first dis-

covered it nesting in some of his trap nests at Lake Placid, Florida.

I wish to acknowledge with sincere appreciation the following individuals who have generously placed on loan or otherwise permitted me to study those specimens pertinent to the present investigation. Drs. Candido Bolívar, Bosque de Chapultepec, México, D.F. (C.B.); California Insect Survey, University of California, Berkeley (C.I.S.); Henry Dietrich, Cornell University (C.U.); R. R. Dreisbach, Midland, Michigan (R.R.D.); Howard E. Evans, Museum of Comparative Zoölogy, Harvard College (M.C.Z.); W. W. Gibson, formerly of The Rockefeller Foundation, México, D.F. (R.F.M.); Karl V. Krombein, U. S. National Museum (U.S.N.M.); C. D. Michener and George W. Byers, University of Kansas (K.U.); T. B. Mitchell, University of North Carolina (U. N. C.); Pe. J. S. Moure, University of Paraná, Curitiba, Brazil (J.S.M.); J. A. G. Rehn Academy of Natural Sciences, Philadelphia (A.N.S.P.); Jerome G. Rozen, Jr., American Museum of Natural History (A.M.N.H.); and P. H. Timberlake, University of California, Riverside (U.C.R.).

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The five species currently included in the subgenus *Xylocopoides* may be distinguished by means of the following key.

Key to the Species of the Subgenus Xylocopoides Michener

1. Males[1] 2
   Females 5
2. Hind basitarsi much longer than corresponding tibiae; outer distal apex of hind tibia armed with two teeth; anterior half of third metasomal tergum not modified as below; antennal sockets situated very nearly midway between upper margin of clypeus and anterior tangent of median ocellus 3
   Hind basitarsi shorter than corresponding tibiae; outer distal apex of hind tibia armed with a single spine-like tooth; anterior half of third metasomal tergum broadly depressed on each side of basally carinate median line, the anterior margin of each depression bearing a transverse row of very long, posteriorly directed, plumose hairs which overlie the depressions (southern México into Costa Rica) *tenuata* Smith

[1] The male of *Xylocopa pallidiscopa* Hurd is unknown.

3. Eyes moderately convergent above, minimum interorbital distance greater than distance across hind ocelli; inner eye margins separated from antennal sockets by more than basal width of scape 4
   Eyes strongly convergent above, minimum interorbital distance much less than distance across hind ocelli (plate VIII, fig. 8); inner eye margins separated from antennal sockets by less than basal width of scape (Maine and Great Lakes region of Canada southward into Florida, westward into Nebraska and Texas) ... *virginica* (Linnaeus)
4. Clypeus normally black, rarely partly maculated with yellow; anterior tibia with the posterior fringe of hairs short, at most approximately as long as maximum tibial width (western United States [Arizona, California, Nevada, New Mexico, Oregon, Texas and Utah] southward into México [Central Plateau including adjacent arid areas and Baja California]) ..... *californica* Cresson
   Clypeus yellow; anterior tibia with the posterior fringe of hairs very long, at least twice the maximum tibial width (southern México) *cyanea* Smith
5. Outer distal apex of hind tibia armed with two teeth; dorsal surfaces of posterior metasomal terga (IV–VI) black pubescent 6
   Outer distal apex of hind tibia armed with a single spine-like tooth; dorsal surfaces of posterior metasomal terga partly (apical margin of IV) or entirely (V and VI) whitish pubescent (southern México into Costa Rica) ..... *tenuata* Smith
6. Distal apex of frontal carina or tubercle extending between antennal sockets and nearly or slightly surpassing their anterior margins; supraclypeal area without a pit just below frontal carina or tubercle 7
   Distal apex of frontal tubercle not or scarcely extending between antennal sockets, situated well before anterior margins of antennal sockets; supraclypeal area with a prominent pit, usually densely filled with pubescence, situated just below frontal tubercle (as in plate VIII, fig. 5) 8
7. Frontal tubercle elevated in the form of a large, longitudinally rounded, laterally compressed prominence; dorsum and sides of thorax thickly clothed with pale pubescence; outer surfaces of middle and hind legs black pubescent, rarely (one instance) are the outer surfaces of hind tibiae and hind tarsi with whitish pubescence (Maine and Great Lakes region of Canada southward into Florida, westward into Nebraska and Texas) ..... *virginica* (Linnaeus)
   Frontal carina linear, its distal apex acuminately pointed; dorsum and sides of thorax thickly clothed with brownish-black pubescence; outer surfaces of middle and hind tarsi as well as hind tibiae clothed with yellowish-white pubescence (central México) ..... *pallidiscopa* Hurd
8. Face exceedingly broad (plate VIII, fig. 5), maximum interorbital distance much greater than intertegular distance; parocular areas densely clothed with very long, and sinuately curved bristles which when viewed laterally suggest a hairbrush (plate VIII, fig. 6); frontal

tubercle bituberculate apically; hind ocelli bounded posteriorly by a precipitously elevated prominence (southern México) .. *cyanea* Smith

Face broad, but not exceedingly so, maximum interorbital distance conspicuously shorter than intertegular distance; parocular areas more sparsely clothed with short, straight hairs, not suggesting a hairbrush when viewed laterally; frontal tubercle simple; hind ocelli not bounded posteriorly by an elevated prominence (western United States [Arizona, California, Nevada, New Mexico, Oregon, Texas, and Utah] southward into México [Central Plateau including adjacent arid areas and Baja California]) ..... *californica* Cresson

Xylocopa virginica (Linnaeus) (Plate VII, figs. 1–4)
(Plate VIII, fig. 8)

Although Smith (1874: 295) and Friese (1902: 198) have recorded this common species of the eastern United States from Cuba, I have not seen specimens from localities beyond the southern tip of Florida (Hurd, 1955: map 1). Possibly the specimens reported by these authors were adventives at the time of their collection. The *Xylocopa* fauna of Cuba, on the basis of my studies, consists of a single species, *X. cubaecola* Lucas, which belongs to the widely distributed and chiefly Neotropical subgenus *Neoxylocopa* Michener. Dover (1924: 147) cites the collection of *X. virginica* from its nesting tunnels in a plank of *Magnolia* intercepted at Nottingham, England.

Recently Moure (1960: 160) has placed *Xylocopa analis* (Fabricius) as a synonym of *X. virginica* proper.

With the addition of the new subspecies decribed below, *X. virginica* is divisible into three geographically allopatric subspecies. These may be separated in the following key.

Key to the Subspecies of Xylocopa virginica (Linnaeus)

1. Males 2
   Females 4
2. Metasomal terga weakly metallic, predominantly black; fourth metasomal tergum without a dorsal, medially interrupted, subapical fringe of whitish hairs 3
   Metasomal terga brilliantly metallic, predominantly green; fourth metasomal tergum with a dorsal, medially interrupted, subapical fringe of whitish hairs (southern Kansas into south central Texas) *texana* Cresson
3. Apical metasomal segments (IV–VII) entirely dark pubescent; dorsum of thorax unicolorously pubescent (Maine and Great Lakes region of

Canada southward into central Florida, westward into Nebraska and Texas) ..... *virginica* (Linnaeus)

Apical metasomal segments (IV–VII), especially ventrolateral sides of terga V and VI, with whitish pubescence; dorsum of thorax predominantly pale pubescent, but with impunctate median surface narrowly surrounded with blackish pubescence (southern Florida) *krombeini* Hurd

4. Metasomal terga weakly metallic, predominantly black, frontal carina less protuberant than outlined below, its summit elevated above rim of antennal socket by less than alveolocellar distance 5

Metasomal terga brilliantly metallic, predominantly green; frontal carina strongly protuberant, its summit elevated above rim of antennal socket by considerably more than alveolocellar distance (southern Kansas into south central Texas) ..... *texana* Cresson

5. Apical metasomal segments (IV–VII) entirely dark pubescent (Maine and Great Lakes region of Canada southward into central Florida, westward into Nebraska and Texas) ..... *virginica* (Linnaeus)

Apical metasomal segments (IV–VI), especially ventrolateral sides of terga V and VI, with whitish pubescence (southern Florida) *krombeini* Hurd

Xylocopa virginica krombeini Hurd, new subspecies

Diagnostic characters.—*Male.* Metasomal terga essentially black, weakly metallic; apical metasomal segments (IV–VII), especially ventrolateral sides of terga V and VI, with whitish pubescence; fourth metasomal tergum without a dorsal, medially interrupted, subapical fringe of whitish hairs; dorsum of thorax predominantly pale pubescent, but with the median impunctate surface narrowly surrounded with brownish or blackish pubescence.

Female.—Metasomal terga similarly colored as male; apical metasomal segments (IV–VI), especially ventrolateral sides of terga V and VI, with whitish pubescence; dorsum of thorax normally uniformly pale pubescent; maximum protuberance of frontal tubercle beyond rim of antennal sockets less than alveolocellar distance.

Holotype male ("Nest B–66, cell 4–5, June 20, 1960"), allotype female ("Nest B–106, mother, June 2, 1960") and five paratypes (♀, Nest B–66, mother, May 19, 1960; ♀, Nest B–189, mother, May 26, 1960; ♀, B–170, mother, June 30, 1960; ♂, Nest B–189, cell 3, June 30, 1960; and ♂, Nest B–66, cell 4–5,

June 10, 1960) from trap nests operated by Dr. Karl V. Krombein at Lake Placid, Highlands Co., Florida. The primary types will be deposited in the collections of the U. S. National Museum (No. 65822). Additional paratypes (52 ♂♂, 26 ♀♀) are designated from the following counties of southern Florida:

Collier Co.: Allen River to Deep Lake, ♂, IV-12-12 (A.M.N.H.). Deep Lake, ♂, IV-13-12 (A.M.N.H.). Everglades, 10–40 miles east, ♂, VIII-30-31, J. C. Bradley and Knorr (C.U.). **Dade Co.:** Everglades National Park, 5 ♂♂, IV-11-61, A. and H. Dietrich (C.U.). Royal Palm State Park, ♂, IV-10-30, G. P. Engelhardt (A.M.N.H.); ♀, III-12, F. M. Jones (A.M.N.H.). **Glades Co.:** Palmdale, 2 ♂♂, 3 ♀♀, II-2-43, M. A. Cazier (A.M.N.H.); ♀, III-29-61, S. W. Frost (U.N.C.); ♂, IV-20-61, A. and H. Dietrich (C.U.). **Highlands Co.:** Archibald Station, Lake Placid, 2 ♂♂, IV-1-47, ♂, IV-10-47, and ♂, II-5-49, J. G. Needham (C.U.); 5 ♂♂, ♀, III-15-61, and ♀, III-19-61, A. and H. Dietrich (C.U.); 2 ♂♂, V-1951 (A.M.N.H.). Lake Placid, ♂, ♀, III-23-61, S. W. Frost (U.N.C.). Highlands Hammock State Park, 4 ♂♂, III-20-55, F. W. Mead (U.N.C.) Sebring, ♂, III-25-38, F. E. Lutz (A.M.N.H.). **Lake Co.:** Eustis, 2 ♀♀, VII-26-22, H. W. Fogg (U.N.C.). **Lee Co.:** ♀, II-28-37 (U.S.N.M.). Olga, ♂, ♀, III-29 to 30-54, H. E. Evans (C.U.). **Manatee Co.:** Oneca, 2 ♂♂, III-24-54, W. W. Boyle (C.U.). **Martin Co.:** Indian Town, 2 ♂♂, III-28-38, F. E. Lutz (A.M.N.H.). Port Sewall, ♀, I-25-39, L. C. and L. J. Sanford (A.M.N.H.). **Okeechobee Co.:** Brighton, 2 ♀♀, IV-7-37, J. C. Bradley (C.U.). Okeechobee, 2 ♂♂, IV-1-37 (A.M.N.H.). **Palm Beach Co.:** Pahokee, 2 ♂♂, V-6-19, F. W. Fattig (C.U.). Palm Beach, 2 ♂♂, ♀, III-1900, and ♂, no date, C. F. Baker (U.S.N.M.). **Pasco Co.:** Lacoochee, 4 ♀♀, VII-7-48, H. W. Crowder (K.U.). **Sarasota Co.:** Myakka River State Park, 7 ♂♂, III-24-24, J. G. Needham (C.U.). Sarasota, ♂, III-24-46, J. G. Needham (C.U.). **Seminole Co.:** ♀, VI-14-55, R. A. Martin (U.N.C.). **Sumter Co.:** Wildwood, 5 ♀♀, VIII-2-30, P. W. Oman and L. D. Tuthill (K.U.). **County:** Haulover, 2 ♂♂, II-24, ♂, no date (U.S.N.M.).

This distinctive subspecies of *Xylocopa virginica* is named in honor of Dr. Karl V. Krombein of the U. S. National Museum who collected the type series in connection with his valuable trap nest studies of North American Hymenoptera. *Xylocopa virginica krombeini* appears to replace *X. virginica s. str.* in southern Florida. In some respects, most noticeably by the whitish pubescence on the ventrolateral margins of the apical metasomal segments, this subspecies is reminiscent of *X. virginica texana*. However, in addition to the wide geographic separation from that subspecies, *X. virginica krombeini* is more

closely allied to *X. virginica* proper in the weakly metallic integument and in the less strongly protuberant frontal tubercle of the female.

One specimen, a female from Paradise Key, Dade Co., Florida (V–16–37, Richard Dow, U.S.N.M.) differs from *X. virginica krombeini* by having the outer surfaces of the hind tibiae and tarsi whitish-yellow pubescent and the apical metasomal sterna are more extensively clothed with whitish pubescence. This specimen has not been included in the type series since it may represent a race confined to the Florida Keys. However, additional specimens will be necessary to establish if this is so or if the aforementioned specimen is an unusual variant of *X. virginica krombeini.*

Xylocopa californica Cresson (Plate VIII, figs. 7, 9)

This species has been divided into three geographically allopatric subspecies (Hurd, 1954, 1955) and the probable mode of species formation in this group of subspecies has been discussed by Hurd (1956) and Hurd and Moure (1961). A systematic account of *X. californica* and its subspecies has been presented earlier (Hurd, 1954, 1955). The following key will serve to distinguish these subspecies.

KEY TO THE SUBSPECIES OF XYLOCOPA CALIFORNICA CRESSON

1. Males 2
   Females 4
2. Metasomal terga predominantly blue; fourth metasomal tergum without a medially interrupted fringe of whitish hairs 3
   Metasomal terga predominantly green; fourth metasomal tergum with a medially interrupted fringe of whitish hairs (North Coast Ranges and Sierra Nevada of California, and southern Cascade Mountains of Oregon) ..... *californica* Cresson
3. Wings heavily infuscated with black and strongly violaceous; metasomal terga dark blue (Deserts of California, Arizona, Nevada, New Mexico, Utah, Texas, and México) ..... *arizonensis* Cresson
   Wings paler, not heavily infuscated with black, less strongly violaceous; metasomal terga blue, often blue with traces of green (Mountains of cismontane northern Lower California and southern California northward to Monterey County) ..... *diamesa* Hurd
4. Metasomal terga predominantly blue 5
   Metasomal terga predominantly green (North Coast Ranges and Sierra Nevada of California, and southern Cascade Mountains of Oregon) *californica* Cresson

5. Wings heavily infuscated with black and strongly violaceous; metasomal terga dark blue (Deserts of California, Arizona, Nevada, New Mexico, Utah, Texas, and México) ..... *arizonensis* Cresson
   Wings paler, not heavily infuscated with black, less strongly violaceous; metasomal terga blue, often blue with traces of green (Mountains of cismontane northern Lower California and southern California northward to Monterey County) ..... *diamesa* Hurd

Xylocopa californica arizonensis Cresson

Until recently, the most southern records of this subspecies, the southernmost subspecies of *Xylocopa californica* Cresson, were Cabo San Lucas, Baja California, México and San Juan de Lagos, Durango, México. The new southermost record, well below the transverse cordillera of central México, is represented by a male and female which were collected at Apatzingan, Michoacan, elevation 1200 feet, on August 7, 1940, " semi-desert scrub " by H. Hoogstraal and K. Knight (A.M.N.H.).

Xylocopa (Xylocopoides) pallidiscopa Hurd, new species

Male.—Unknown.

Female.—Length 24–28 mm. Forewing including tegula 21–23 mm. Integument predominantly black, paler below, weakly metallic blue on head, dorsum and sides of thorax, metasomal terga, and outer surfaces of fore and middle tibiae, elsewhere at most only feebly metallic. Pubescence short, thickest on thorax and undersurfaces of metasoma, sparser on head, and scarcely evident on dorsal surfaces of metasomal terga; vestiture chiefly brownish-black but with conspicuous whitish pubescence on ventrolateral portions of apical metasomal segments and with yellowish-white pubescence on outer surfaces of hind tibiae and tarsi and middle tarsi.

Eyes as convergent above as below (63 : 63), maximum interorbital distance slightly greater than length of eye (74 : 72), but considerably shorter than intertegular distance (74 : 104); clypeus approximately one-half as long as broad (29 : 61), equal in length to clypeocellar distance (29 : 29); interocellar distance shorter than ocellorbital distance (13 : 16); orbitoccipital distance much shorter than ocelloccipital distance (19 : 25); interalveolar distance equaling alveolorbital distance (19 : 19); first flagellar segment very nearly equal to combined length of succeeding three segments (15 : 5 : 6 : 6); ocelli without adjacent prominences.

Frontal carina elongate, cariniform, longitudinally sulcate, its distal apex clearly elevated above level of supraclypeal area, projecting slightly beyond anterior margins of antennal sockets and situated well beyond one-half the clypeocellar distance (19 : 29); supraclypeal area without a pit below distal apex of frontal carina.

Outer distal apex of hind tibiae each armed with two teeth; extreme distal apex of basitibial plate situated considerably beyond middle of tibia (52:83).

Prepygidial area very similar to that of *X. californica* (plate VIII, fig. 7).

Holotype female and one paratype collected at seven miles northeast of Jacala, 5000 feet, Hidalgo, México on July 27, 1954 by a University of Kansas Mexican Expedition and are deposited in the collections of that institution. One additional paratype was taken at Jacala, 4500 feet, Hidalgo, México by Ralph Haag on June 21, 1939 and is in the collections of the Museum of Comparative Zoölogy, Harvard University.

Superficially the female of *Xylocopa pallidiscopa* closely resembles *X. californica*, especially the subspecies *arizonensis*, in general colorational features. Structurally, however, it is more closely allied to *X. virginica* by the absence of the pit immediately below the distal apex of the frontal carina, a striking characteristic of *X. californica* and *X. cyanea* (plate VIII, fig. 5). It differs most noticably from *X. virginica* by the elongately cariniform frontal carina, and by the pale pubescence on the outer surfaces of the hind tibiae and tarsi and middle tarsi. The male is unknown.

Xylocopa cyanea Smith (Plate VIII, figs. 5–6)

Xylocopa cyanea Smith, 1874, Trans. Ent. Soc. London, pp. 296–297 (male, "Mexico"); Cresson, 1879, Trans. Amer. Ent. Soc., 7: 228 (male, Mexico); Cockerell, 1899, Biblioteca Agric. Secy. Fomento, Mexico, 15: 18 (Mexico); Maidl, 1912, Ann. K. K. Naturhist. Hofmus. Wien, 26: 318–319 (male, female, Mexico).

Xylocopa singularis Pérez, 1901, Act. Soc. Linn. Bordeaux, 56: 111–112, 116–120 (male, female, "Mexique"), *teste* Maidl, 1912: 318.

The curiously modified head of the female (plate VIII, figs. 5, 6) is unique among the *Xylocopa* of the world. Nothing is known concerning its nesting habits and consequently it is not known whether the modified head is an adaptive response to its nesting habit.

This species, previously listed only from "Mexico" or "Mexique", is now recorded from seven states and the federal district of Mexico:

D.F.: El Guarda, 15 miles south, ♀, XI-14-46, F. E. Skinner (U.C.R.). Ixtapan de la Sal, 5500 ft., ♂, VIII-9-54 (K.U. Mexican Expedition). **Guerrero:** Taxco, 8 miles north, ♂, VIII-8-54 (K.U. Mexican Expedition). **Michoacan:** Cuidad Hidalgo, 6400 ft., ♀, VI-16-53 (K.U. Mexican Expedition). Tancitaro, 6000 ft., ♀, VII-24-41, H. Hoogstraal (A.M.N.H.). **Morelos:** Tepoztlan, 2 ♂♂, 6 ♀♀, VIII-20-56, R. and K. Dreisbach (R.R.D.). Cuernavaca, 6000 ft., ♀, II-7-54, R. R. Dreisbach (R.R.D.). Cuernavaca, 3 miles northwest, 6500 ft., ♀, VI-28-59, H. E. Evans (C.U.). Malinalco, 2 ♂♂, VIII-1943, C. Bolivar (C.B.). **Nyarit:** Tepic, ♀, VIII-22-05, P. H. Goldsmith (M.C.Z.). **Oaxaca:** Totalapan, 5 miles northwest, ♂, VII-6-53 (K.U. Mexican Expedition). Camaron, 20 miles east, ♀, VII-20-56, J. W. MacSwain (C.I.S.). **Puebla:** Environs of Tehuacan, ♂, 1903, L. Diguet (J.S.M.). **Vera Cruz:** "Mex. 1785" [= Medellin], ♀, C. F. Baker (U.S.N.M.).

Xylocopa tenuata Smith

Xylocopa tenuata Smith, 1874, Trans. Ent. Soc. London, p. 299 (female, "Mexico"); Cresson, 1879, Trans. Amer. Ent. Soc., 7: 228 (female, Mexico); Cockerell, 1899, Biblioteca Agric. Secy. Fomento, Mexico, 15: 18 (Mexico).

Xylocopa albocaudata Friese, 1925, Stettiner Ent. Zeitg., 86: 16 (female, "San José de Costa Rica"). **New synonymy.**

The male of *Xylocopa tenuata* Smith, previously unknown, may be easily recognized by the remarkably and unusually modified third metasomal tergum. The anterior half of this tergum is broadly depressed on each side of the basally carinate median line and the anterior margin of each depression bears a transverse row of very long, posteriorly directed, plumose hairs which overlie the depressions. The female was first described by Smith (1874: 299) from "Mexico". Later it was described again as a new species, *X. albocaudata* Friese (1925: 16), on the basis of "2 ♀ von San José de Costa Rica." A study of the type specimen of *X. tenuata* by Padre J. S. Moure and a subsequent comparison by us of his study notes with a specimen (♀, San José, Costa Rica, July 1923, A.M.N.H.) determined by Friese as *X. albocaudata* reveals this new synonymy.

Previous to the following records, *X. tenuata* Smith was known only from San José, Costa Rica and "Mexico".

Costa Rica: Mt. Redondo, ♂, I-1903 (A.N.S.P.). **México:** Cuernavaca, Morelos including C. F. Baker equivalent [Mex. 2499], 2 ♂♂, no date, C. F. Baker (U.S.N.M.); ♀, IX-1923, E. G. Smyth (U.S.N.M.). Cuatla, Puebla, ♂, X-29-22, E. G. Smyth (U.S.N.M.). Hacienda de la Imagen,

Guerrero, 4000 ft., ♂, no date, H. H. Smith (J.S.M.). Teloloapan, Gro., ♀, VIII-21-57, D. Douglas (R.F.M.). Cacahuamilpa, Gro., 2 ♂♂, X-5 to 9-58, G. Halfter and E. G. Mathews (C.U.).

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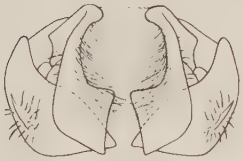
Explanation of Figures

Plate VII

Figs. 1–4, genitalia of *Xylocopa virginica* (Linnaeus), male.
- Fig. 1, posterior view.
- Fig. 2, lateral view.
- Fig. 3, dorsal view.
- Fig. 4, ventral view.

Plate VIII

Figs. 5–6, head of *Xylocopa cyanea* Smith, female.
- Fig. 5, anterior view.
- Fig. 6, lateral view.
- Fig. 7, pygidial area of *X. californica* Cresson, female.
- Fig. 8, head of *X. virginica* (Linnaeus), anterior view, male.
- Fig. 9, hind tibia of *X. californica* Cresson, lateral view, female.



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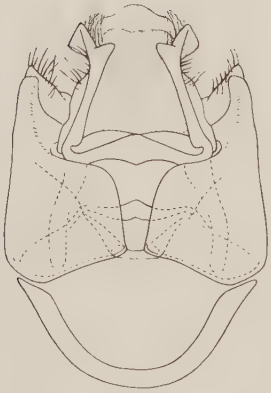

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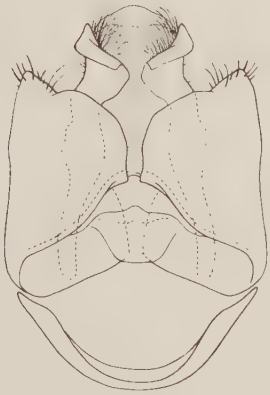

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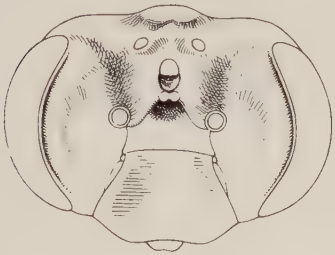
HURD: CARPENTER BEES



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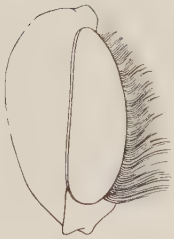

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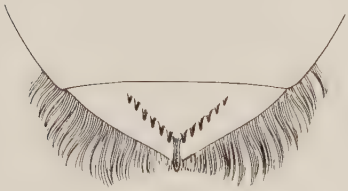

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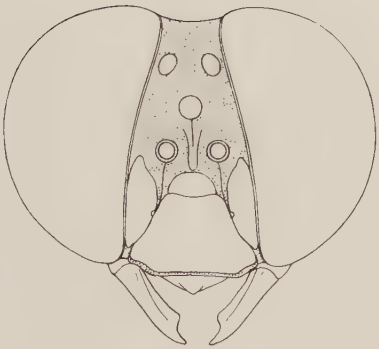

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HURD: CARPENTER BEES

SYSTEMATIC AND MORPHOLOGICAL NOTES ON NORTH AMERICAN CONOTYLOID DIPLOPODA

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Since the publication in 1895 of the excellent monograph on North American chordeumoids by O. F. Cook and G. N. Collins, very little basically useful work on our fauna has appeared. In 1895 the number of known species was 27, distributed among ten genera, whereas the most recent listing (Chamberlin and Hoffman, 1958) shows that the total has increased to 86 species and 26 genera, now allocated to nine different families. Yet this increase is due entirely to papers in which new forms are described with an absolute minimum of attention to detail, the descriptions sometimes being adequate for later recognition of species but not for an understanding of their structure and relationships. To the best of my knowledge only one attempt has ever been made to provide keys for identification of the rising number of species (Loomis, 1943).

Upon recently having occasion to work with chordeumoids, I was astonished at the taxonomic condition of Nearctic forms in comparision with the detailed knowledge of European species. Putting our fauna in a more satisfactory position is obviously a large order, and for many reasons a task which can best be accomplished by cooperative efforts. Since a complete revision of the group, however desirable, must still be far in the future, two immediate measures can be undertaken. First would be a drastic improvement in the quality of descriptions and particularly of illustrations; second, piecemeal attacks on various genera or groups of genera as material becomes available.

I am concerned at the present with a number of genera that have been referred to the family Conotylidae without serious consideration of their characters, which in general have remained unknown. Some attempt is made to settle the relationships of these groups and to clarify structural details which must form the basis of any classification. In evaluating the relative taxonomic importance of secondary sexual characters of the males,

reference must inevitably be made to the high standard set by the European specialists Verhoeff, Brolemann, and Ribaut. These investigators have defined and named virtually every structural detail of possible taxonomic utility.

All of the American genera of Chordeumida were placed by Cook and Collins in the single family Craspedosomatidae. Cook soon realized that the genera were far too diverse to be comprehended within a natural family group, for in the following year he published a revised system of chordeumoid families which were more limited in scope, erecting a family Cleidogonidae for *Cleidogona, Bactropus,* and *Pseudotremia;* Conotylidae for *Conotyla, Trichopetalum, Zygonopus,* and *Scoterpes;* and Branneriidae for *Branneria.* The remaining genera *Caseya* and *Underwoodia* were moved from the Craspedosomatidae to the Chordeumatidae. Cook's definition of the Conotylidae was framed largely from characters of the 9th pair of legs.

In 1913, Karl W. Verhoeff proposed a genus *Japanosoma,* which, on the basis of Cook and Collins' paper, he considered to belong to the Conotylidae. At the same time he referred the Neotropical genera *Eudigona* and *Apodigona* of Silvestri to the same family, and prepared a provisional classification which recognized three subfamilies, namely Conotylinae, Japanosominae, and Trichopetalinae, the first two monotypic, the last with four genera.

Verhoeff's key to genera was subsequently adopted almost *verbatim* by Attems (1926), who omitted only the subfamily names; and it was later copied by Verhoeff himself in the systematic section of his great volume in Bronn's *Klassen und Ordnungen des Tierreichs* series (1926–1932). Here, however, although the arrangement had not been changed for several decades, Verhoeff admitted the inadequacy of his groupings, and remarked that the Japanosominae might best be elevated to family rank, taking with it the two genera *Eudigona* and *Apodigona.* Shortly after completion of his manuscript, Verhoeff received chordeumoid material from the United States, including specimens of *Trichopetalum* and of a new genus which he called *Proconotyla.* In publishing his findings (1932) Verhoeff called attention to the

considerable differences between the two genera mentioned, erecting a new family Trichopetalidae and a new superfamily Americopoda to receive it. Both of these categories were unfortunately overlooked by the compilers of the "Checklist of the millipeds of North America."

Since 1932, seven new "conotylid" genera have been set up for North American species, nearly all of them inadequately described and illustrated; several even being based upon female specimens. In the latter case, such generic names cannot be definitely included in the Conotylidae, a family which like most others of the order is defined principally upon the basis of male genitalia. As I have been able to determine, even some of these genera originally based on males have fared little better, having been proposed after little or no careful study and which, in actuality, are not even confamiliar with *Conotyla!*

It is generally recognized that the anterior legs of males in the Chordeumida are subject to remarkable variation and modification associated with sexual functions. In some cases as many of four leg pairs may be involved in the gonopod complex. Generally, however, only the two leg pairs of the 7th body segment are so adapted, and their specializations may become very complicated. Ribaut and Brolemann have performed a great service in developing a terminology by which the various parts of the gonopods can be designated, and it follows naturally that if the classification of any group is based exclusively upon a given structure, every effort should be made to understand that structure as fully as possible.

Insofar as the Conotylidae is concerned, most of the Brolemann-Ribaut names are not applicable, as the special modifications (such as angiocoxite, cheirite, and others) do not seem to be developed. Nonetheless, one significant distinction made by Brolemann is of considerable immediate interest as a fundamental refinement of concept. He defined (1935) two basic arrangements of the gonopods:

1. The posterior leg pair (9th) of the 7th segment functions as true gonopods, the legs of the anterior pair (8th) being modified into protective or shielding structures called *peltogonopods.*

2. The anterior leg pair of the 7th segment assumes the major role in sperm transfer and carries the name gonopod, while the posterior pair is modified for retention of the seminal fluid, and designated as *paragonopods.*

Aside from these major distinctions, the individual pairs of gonopods are subject to considerable morphological diversity, particularly as regards the sternite of the 8th legpair. And on the basis of gonopod structure, the family Conotylidae in the collective sense of American authors can be divided into *at least* two distinctive families which compare favorably with the corresponding groups recognized by European workers. As thus restricted, the resulting generic groups are more natural ensembles, strongly resembling each other in body form and general habitus. It is felt that the recognition of such families at this time is a most desirable step, both as regards the achievement of a natural classification and as a means of emphasizing taxonomic characters heretofore ignored by American students of the Diplopoda. It is to be hoped that those fortunate enough to obtain material of other Nearctic chordeumoid genera will endeavor to elucidate these characters, as part of the necessary overture to an eventual synthesis and revision of the entire Chordeumida.

The following key is designed only to emphasize the major structural differences between the two families here segregated from the old Conotylidae.

1. Body moderate in size 8–20 mm. in length, well pigmented; the ocelli numerous, in a pigmented triangular ocellarium; antennae slender, elongate; 8th legpair of males modified as peltogonopods, often severely reduced in size and structure, composed of a single article; 9th legpair modified as gonopods, with 3 articles, the coxae large and usually strongly produced distad, in contact medially or nearly so; coxae of 10th legpair perforated for the accommodation of eversible coxal vesicles ..... Conotylidae Cook, 1896

   Body small, less than 10 mm. in length, usually white or clear testaceous; ocelli fewer, usually less than 10, in two or three rows in an L-shaped ocellarium, or absent; antennae distinctly short and clavate, the 5th article particularly enlarged; 8th pair of legs of males modified as gonopods, large and complex in structure, with distinct coxal and femoral elements; 9th pair of legs modified as paragonopods, composed of two articles, the coxae simple and widely separated by the broad sternite; coxae of 10th and 11th pairs of legs perforated by the broadly expansible coxal vesicles

   Trichopetalidae Verhoeff, 1932

Of the twelve genera placed in the "Conotylidae" in the Checklist, only three are now so allocated, the others belonging either with the Trichopetalidae or some other family not presently defined. *Conotyla* itself has become something of a catch-all genus, and probably many of the western species will be found not congeneric with *C. fischeri*. Bollman's species *atrolineata* seems clearly to represent a distinct generic type. The species named *C. montivaga* by Loomis (1943) has been restudied from a paratype, and is here made the type species of a new genus. Such entities as *Bollmanella oregona* Chamberlin and *Cookella leibergi* (Cook and Collins), known only from females, may not even be Conotylidae at all.

The genera of the Trichopetalidae will be taken up in a subsequent paper. They include *Trichopetalum* Harger (of which *Tynopus* Chamberlin is doubtless a synonym), *Flagellopetalum* Causey, *Trigenotyla* Causey, *Zygonopus* Ryder, and perhaps also *Scoterpes* Cope, although there is some basis for the inclusion of the last-named in a family of its own.

Family CONOTYLIDAE Cook

Conotylidae Cook, 1896, Brandtia, No. 2: 8. Verhoeff, 1932, Zool. Jahrb., Abt. Syst. 62: 500.

Chordeumidea of typical form as regards body form, collum, telson, antennae, and mouthparts. Body with 30 segments, these with prominent paranota except on antepenultimate; ocelli 15–25, pigmented, in a triangular cluster; antennae long and slender, usual lengths of the articles in decreasing order: 3-5-6-2-1-7; mandibles with 11 pectinate lamellae; mentum undivided. 8th legs of males modified as peltogonopods, simple, often reduced in size, consisting of a single article with a characteristic coxal pocket on the lateral side at base, the sternite reduced but not otherwise modified; 9th legs modified as gonopods, with three articles, the coxae enlarged and variously specialized, 2nd article abruptly clavate, 3rd elongate oval, cylindrical, glandular, without a pretarsus.

The genitalia of conotylid diplopods have been poorly understood by most investigators, with the result that some have even regarded the 9th legpair as distinct from the posterior gonopods despite the morphological difficulties of such an interpretation. The first reference to this general subject, however, is not far from the truth: "In dissecting *C. fischeri* we found that the posterior pair of genital processes always remained attached to

the ninth pair of legs, while the anterior pair remained in the body . . ." (Cook and Collins, 1895: 71). An investigation of the matter, made with particular emphasis on the musculature of the gonopod apparatus, shows fairly clearly, I think, that the so-called "posterior gonopods" are in reality the *modified coxae of the 9th legpair,* and that these legs are therefore composed of three articles instead of two as traditionally conceived. Furthermore, as the homology seems clear enough, I judge that the enlarged and produced part of these coxae represents the extruded and sclerotized coxal vesicle. I herewith propose the use of Brolemann's term "colpocoxite" which was originally defined to denominate just such a development.

Since the origin of gonopods from functional walking legs of the 7th segment is nowhere more clearly shown than in platydesmid and chordeumoid diplopods, homologies in musculature in these groups is most instructive. It will be recalled that the motivation of each leg is supplied by coxal muscles which originate on the sternal (tracheal) apodemes on *both* sides of the body. On the anterior side of each sternal complex, there is a large deltoid muscle (*remotor coxae longus*) which originates on the inner face of the sternal apodeme and inserts on the mesial edge of the base of the coxa of the opposite side. This muscle provides a good reference point, as it occurs likewise in the gonopods of both 7th and 8th pairs of legs although reduced in size. As can be seen from the figures (particularly figure 4) these muscles insert on the base of the so-called posterior gonopods of the opposite sides exactly as in the adjoining walking legs. There is no longer much mobility in these coxae, and no muscles from them into the telopodite articles of the 9th legs, but the structural relationships here are clear enough. The interested reader is referred to the excellent paper of Manton (1958), particularly to figures 19–21, for comparison with Plate IX, fig. 4 of this paper.

Cook and Collins stated that the 10th and 11th leg pairs have the coxae perforated, but I have been unable to confirm the presence of coxal sacs on the 11th legs in the material I have seen, nor did Verhoeff detect them in *Proconotyla.* The coxae of the 10th legs, however, are greatly enlarged (about twice as

large as those following) and contain eversible pouches, upon which the distal ends of the recurved colpocoxites rest.

Since genera are defined largely upon modifications of the genitalia, verbal key characterizations are often difficult to phrase, and usually add nothing to the visual concept gained from illustrations. As but four genera are here admitted to the family Conotylidae, I believe that reference to the drawings will be sufficient for generic recognition *in lieu* of a dichotomic key.

Genus **CONOTYLA** Cook and Collins

Conotyla Cook and Collins, 1895, Ann. New York Acad. Sci. 9: 70. (*Type species, C. fischeri* Cook and Collins, by original designation.)

Diagnosis.—Peltogonopods short, divergent distally, with a subterminal projection or remnant thereof which extends caudad between the colpocoxites and telopodites of the gonopods, latter with elongate coxal processes modified as colpocoxites, extending distad beyond end of the second article of the legs, and provided on their caudal surface with a small field of fine setae or pubescence.

Fourth podomere of the 4th and 5th pairs of legs of males with a subconical process on the ventral side; 6th legs unmodified; 7th legs with or without modification of the 4th podomere.

Species.—Of the 13 species admitted to *Conotyla* in the "Checklist" I believe that only two are congeneric with *C. fischeri.* Two additional species are named in the following pages. The so-called *Conotyla* species from central and western North America are doubtless all referable to other genera, and a start toward their eventual re-allocation is made here.

Distribution.—Appalachian region from New York south to Virginia, west into Indiana. Females have been taken in the mountains of North Carolina and Tennessee, and the genus probably extends as far south as Georgia and Alabama. Undoubtedly, a large number of species remain to be diagnosed and named.

Conotyla fischeri Cook and Collins (Plate IX, fig. 7)

Conotyla fischeri Cook and Collins, 1895, Ann. New York Acad. Sci. 9: 71, figs. 55–78.

This species was originally described from six localities in three counties in central western New York. The vicinity of

Syracuse, Onondaga County, has recently been selected as the restricted type locality (Chamberlin and Hoffman, 1958: 99). It is of interest to record an additional collection of the species, which apparently has not been reported since 1895.

New York.—Hamilton County, two miles west of Morehouseville, October 30, 1955, Leslie Hubricht, leg.

The illustrations of *fischeri* published with the original description leave very little to be desired. However, I give at this time a drawing of the peltogonopods, in caudal aspect, for comparison with those of the two new species from Virginia.

The proximally directed process on the 4th podomere of the 7th pair of legs is apparently unique to *fischeri.*

Conotyla melinda new species (Plate IX, figs. 4–6)

Type specimens.—Male holotype and female paratype, U. S. Nat. Mus. Diplopod Type No. D-616, from oak woods along crest of Brush Mountain, two miles west of Blacksburg, Montgomery County, Virginia, December 5, 1960, R. L. Hoffman.

Diagnosis.—Peltogonopods short, robust, distally bent laterad and then caudad, thence bearing erect, slender, terminally plumose processes which in situ extend caudad behind the bases of the gonopods (figure 6). Gonopods with large, stout colpocoxites, these curved caudad distally and rather abruptly terminating, the caudal side of each with a thin median vertical crest with a field of short setae along its base on the lateral side. Figure 4 shows the arrangement of the gonopodal musculature, as well as the nature of the sternum and stigmata.

Similar in size and general body structure to *Conotyla fischeri,* differing largely in the absence of a process from the 4th podomere of the 7th pair of legs of the male.

Distribution.—Apparently widespread in southwestern Virginia. Aside from the type locality, *C. melinda* has been collected at the following localities.

Virginia: *Craig County;* oak woods along State Hy. 42, near Sinking Creek School, March 15, 1956 (in copula). *Giles County;* sinkhole beside U. S. Hy. 460, between Newport and Pembroke, November 30, 1953, L. Hubricht and R. L. Hoffman, legg. Rhododendron thicket on headwaters of Little Stony Creek, Salt Pond Mountain about 3 miles north of Mountain Lake P. O., October 10, 1955, R. L. and R. B. Hoffman, legg. *Patrick County;* in rhododendron thicket, Dan River Gorge, about 5 miles southwest of Vesta, November 25, 1950.

The presently known range of this species coincides very closely with that of the xystodesmid *Nannaria wilsoni* Hoffman; both

species probably extend into the adjoining states of West Virginia and North Carolina.

Conotyla venetia new species (Plate IX, figs. 1–3)

Type specimens.—Male holotype and paratypes of both sexes, U. S. Nat. Mus. Diplopod Type No. D-593, from oak woods three miles north of Clifton Forge, Alleghany County, Virginia, December 3, 1949, R. L. Hoffman.

Diagnosis.—Peltogonopods short, robust, divaricate, with a laterally directed subterminal lamina and a long slender, distally enlarged and uncate process which extends caudad to grasp the colpocoxite of the gonopod (figure 3). Gonopods large and stout, the colpocoxite robust and curved caudad, terminating in a broad, thin, caudolaterally directed lamina and a slender, curved, terminal process; a small field of fine, dense pubescence on the lateral side at about the midlength—a modification implicated with the passage of the terminal process of the peltogonopods (figures 1, 2). Sternite of gonopods produced medially into a small bilobed condyle between the coxobases. 4th and 5th pairs of male legs with a small pulvillar lobe on the ventral side of the 4th podomere; 7th pair of legs without modifications.

Structure similar to that of *C. fischeri;* size moderate, up to 15 mm. in length; ocellaria well-developed, with about 20 ocelli in four rows forming a triangular patch.

Distribution.—Aside from the type locality, this species is known only from Big Knob (4000 feet) on Warm Spring Mountain, six miles north of Covington, Alleghany County, Virginia, where specimens were taken on May 5, 1950, by L. Hubricht and me. *C. venetia* is thus known to range vertically at least over 3000 feet, and doubtless will be found to occur over much of central western Virginia.

SONORATYLA new genus

Type species.—*Conotyla montivaga* Loomis, 1943.

Diagnosis.—Peltogonopods simple, in the form of moderately large suboval flattened structures with a laciniate process or elongate fringe on the caudal surface, but not produced into a caudally directed branch extending behind the colpocoxites of the gonopods. Latter of the usual form typical for the family, the distal article perhaps smaller than usual, colpocoxite small, in the form of a thin concave lamina much shorter than the second gonopodal article.

Anterior legs of males with ventral processes or lobes present or best defined only on 4th podomeres of the 3rd and 4th pairs.

Remarks.—The simple structure of the genitalia which is characteristic of *montivaga* appears to recur also in some other

known species, the similarity suggesting a natural group worthy of generic recognition. In the better-documented forms, the location of processes on the pregonopodal limbs appears to provide confirmatory data. The several conotylid species thus endowed range widely over central and southern United States, occupying an area apparently to the exclusion of the more strictly Appalachian range of *Conotyla*. A restudy of the species which are here somewhat provisionally assigned to *Sonoratyla* is much to be desired.

Species.—Four, listed as follows.

Sonoratyla montivaga (Loomis) new combination (Plate X, figs. 10–11)

Conotyla montivaga Loomis, 1943, Bull. Mus. Comp. Zool. 92, No. 7: 383, fig. 4a–d.

The species is known from three localities in Arizona and New Mexico. A specimen from Gunnison, Colorado (D. Lindsley, leg.) is similar to typical material and may represent a more northern population of the species. *S. montivaga* appears to be closely related to the following form (which needs careful restudy); perhaps the Colorado population is intermediate between them.

The accompanying illustrations were made from a male paratype, U. S. Nat. Mus. Diplopod Type No. D-271.

Sonoratyla deseretae (Chamberlin), new Combination

Conotyla deseretae Chamberlin, 1910, Ann. Ent. Soc. America, 3: 235, pl. 31, figs. 3–8; pl. 32, figs. 1–7.

The original description of *deseretae* is long and detailed; only the genitalia require restudy. As illustrated, the gonopods (9th legs) are shown to have no coxal or sternal elements, but this is perhaps due to disassociation during dissection. I believe that the genitalia will be found to resemble those of *montivaga* closely.

Sonoratyla pectinata (Causey) new combination

Conotyla pectinata Causey, 1952, Proc. Biol. Soc. Washington, 65: 112, figs. 4, 5.

The species is apparently still known only from the defective male holotype, collected in Carroll County, Illinois. The present

combination is somewhat tentative, but the form of the genitalia strongly suggests affinity with *S. montivaga*.

Sonoratyla specus (Loomis) new combination

Conotyla specus Loomis, 1939, Bull. Mus. Comp. Zool. 86: 184, figs. 11a–c; 1943, idem, 92: 382. Causey, 1952, Proc. Biol. Soc. Washington, 65: 113.

S. specus has been collected at numerous localities in eastern Missouri and adjacent parts of Illinois. Loomis (1943: 383) has already remarked on the relationship of this species to his *montivaga*.

Genus **TAIYUTYLA** Chamberlin

Taiyutyla Chamberlin, 1952, Chicago Acad. Sci., Nat. Hist. Misc., No. 113: 1. (*Type species, T. corvallis* Chamberlin, by original designation.)

Diagnosis.—Peltogonopods very long and flattened, with a large and well-formed sternum, the latter produced at the median line into a triangular lobe connecting the coxal areas of the peltogonopods; lateral basal pockets conspicuous; distally the appendages are provided with slender, acicular subterminal processes. Gonopods large and robust, the colpocoxites long and slender, each with a slender, curved subterminal process on the caudal side which is partially concealed in anterior aspect by a translucent hyaline plate. Gonopods composed of the usual two articles distad of the colpocoxite. Males with a prominent subconical process on the ventral side of the 4th podomere of the 4th to 7th pairs of legs. Ocelli pigmented, the ocellarium subtriangular in shape, composed of three rows of ocelli.

Species.—Two.

Distribution.—Known only from western Oregon.

Remarks.—The original description of this genus appears to be in error with respect to the structure of the genitalia, particularly in stating "Anterior gonopods united at base with the posterior, complicated in structure, presenting two principal and subequal branches." Through the kindness of Vincent D. Roth, collector of the type series, I have received a male topotype which is almost certainly conspecific with the types of *corvallis*. The drawings made from this specimen (figures 8–9) indicate that the male genitalia are typically conotyloid, but not biramous as indicated by the original illustrations. Presumably that drawing was made from a slide mount in which the peltogonopods and gonopods were superimposed in some way (perhaps not separated in the dissection). By superimposing sketches of the

two pairs of appendages taken from my topotype, an effect almost identical with that shown in Chamberlin's figure 1 can be achieved. This clarification of structure of course nulifies the additional point of presumed difference between *Taiyutyla* and *Conotyla* (i.e., that the " ninth legs " of the former having three articles instead of two). Nonetheless, I think that the genitalia provide ample basis for generic separation. Perhaps some of the western species described in *Conotyla* actually will be found referable to this genus.

Taiyutyla corvallis Chamberlin (Plate X, figs. 8–9)

Taiyutyla corvallis Chamberlin, 1952, Chicago Acad. Sci. Nat. Hist. Misc., No. 113: 1, figs. 1, 2.

This species is somewhat smaller in size than the average for species *Conotyla*, but the general body form and appearance is much the same.

The coxal cavity of the peltogonopods is particularly distinct, and is perhaps homologous to the eversible coxal vesicles of the normal ambulatory legs. There is some indication that this cavity merges into a groove running out to the terminal process, but the condition could not be verified with the single slide mount at hand. In general, the peltogonopod complex is much less reduced than in the species of *Conotyla*, and may reflect a less specialized condition of the genitalia.

Taiyutyla jonesi (Chamberlin), new combination

Conotyla jonesi Chamberlin, 1951, Chicago Acad. Sci. Nat. Hist. Misc., No. 87: 6, figs. 12, 13.

I believe that the appearance of the " gonopod " as shown in the original figures is due once again to inadvertant superposition of both pairs of genitalia as discussed for the preceeding species, and think that a restudy will show *jonesi* to be structurally similar to *corvallis*. Both forms occur in western Oregon.

Genus **PROCONOTYLA** Verhoeff

Proconotyla Verhoeff, 1932, Zool. Jahrb., Abt. Syst. 62: 501. (*Type species, P. blakei* Verhoeff, by monotypy.)

This genus is provisionally admitted as valid, although the genitalia suggest affinity with such forms as *Conotyla bollmani*

and *C. vaga*. The peltogonopods, at any rate, are long and slender, almost of the form seen in *Taiyutyla*, and apparently are not provided with posterior processes which extend back around the colpocoxites. I have seen the type slide of *P. blakei* (in the Zoologisches Staatssammlung, München), but because of its rather indifferent condition I can not improve upon the drawings published by Verhoeff. The study of topotypes of *blakei* is much to be desired.

Procontyla blakei Verhoeff

Proconotyla blakei Verhoeff, 1932, Zool. Jahrb. Abt. Syst. 62: 501, pl. 5, figs. 33–37; pl. 6, fig. 38.

Known only from the type locality, Mount Adams in Essex County, New York, and possibly endemic to the higher peaks of the Adirondacks.

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Explanation of Figures

Plate IX

Fig. 1.—*Conotyla venetia* n. sp., colpocoxites of gonopods (9th legs), oral aspect, male topoparatype.

Fig. 2.—*Conotyla venetia* n. sp., colpocoxites and 9th leg, aboral aspect, male topoparatype.

Fig. 3.—*Conotyla venetia* n. sp., peltogonopods, aboral aspect, male topoparatype.

Fig. 4.—*Conotyla melinda* n. sp., gonopods with associated musculature, oral aspect, male topoparatype.

Fig. 5.—*Conotyla melinda* n. sp., gonopods, aboral aspect, male topoparatype.

Fig. 6.—*Conotyla melinda* n. sp., peltogonopods, aboral aspect, male topoparatype.

Fig. 7.—*Conotyla fischeri* Cook and Collins, peltogonopods, aboral aspect. (Figs. 1–7 all drawn to same scale.)

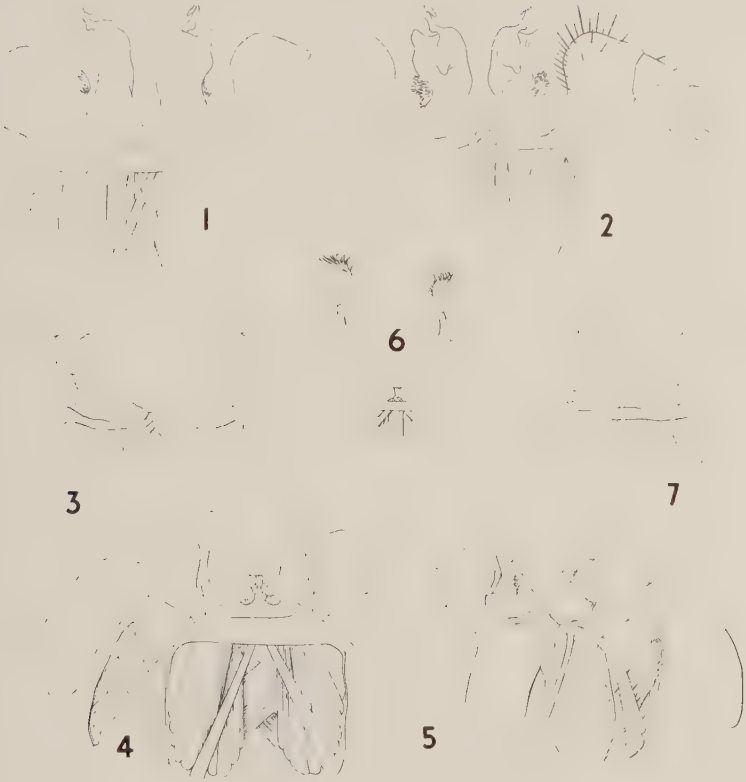
Plate X

Fig. 8.—*Taiyutyla corvallis* Chamberlin, peltogonopods, aboral aspect, male topotype.

Fig. 9.—*Taiyutyla corvallis* Chamberlin, gonopods, oral aspect, male topotype.

Fig. 10.—*Sonoratyla montivaga* Loomis, peltogonopods, aboral aspect, male paratype.

Fig. 11.—*Sonoratyla montivaga* Loomis, gonopods, oral aspect, male paratype.



HOFFMAN: CONOTYLOID DIPLOPODA

HOFFMAN: CONOTYLOID DIPLOPODA

INSECT METAMORPHOSIS AND RETROMORPHOSIS

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When the caterpillar first became famous for "turning into a butterfly," very probably it was not known that the caterpillar hatches from a butterfly's egg and is merely a young butterfly. Its transformation, therefore, was viewed as an actual case of one creature being metamorphosed into another, a popular theme in the fiction of ancient writers. So, when it was found that many other insects go through a similar transformation, the term "metamorphosis" became adopted in entomology to designate the change of form from larva to adult.

We now realize, however, that it is the young butterfly that has been transmuted into a caterpillar, and the same is true for other young insects that have become larvae differing radically from their parents. On the other hand, the change of the young insect into the adult is simply a reversion to the parental form, which alone can propagate the species. We, therefore, have two changes of form in the life of the insect, each of which may be termed a metamorphosis, though the two are entirely unlike in nature. Since the second transformation is a necessary consequence of the first, it will be of interest to speculate on why and how the young insect has come to differ so much from its parents.

Certainly we must assume that the young of all insects originally resembled their parents at least as much as does the modern young grasshopper or young cockroach. With these insects the young differ from the adults mostly in matters of immaturity, such as the imperfect condition of the wings and genital organs, or in the general form and proportions of the parts of the body. The young and adults live together in the same habitat and feed on the same kind of food with the same kind of mouth parts. There is no reason why they should differ.

The plight of the young insect, however, is quite different in the case of those species in which the adult has taken advantage

of its wings to explore the environment and has developed mouth parts for a kind of diet that would be entirely inaccessible to the flightless young. The young insect in this case would be left to starve if it had to inherit the newly acquired structure and feeding organs of its parents. Hence, the usual laws of inheritance have been set aside allowing the young insect to follow an evolutionary course of its own, by which it has become structurally adapted to some suitable habitat and for feeding on the food there available. Thus the young insect has become a larva often very different from its parents by a change of form that took place somewhere in the evolution of its species. This primary metamorphosis that produced the larva, however, is very different from the secondary metamorphosis by which each individual returns to the parental form.

The way by which insects have become structurally adapted to special environments is difficult to visualize. The environment itself is only a passive mold to which the insect becomes adjusted. The adoption of a liquid diet could not cause the mouth parts to form a proboscis; life in the water could not produce gills. New characters must have been acquired by a series of favorable gene mutations. A flat larva might readily become a leaf miner, a cylindrical larva a borer or a burrower, but it is improbable that preadaptation ever produced a mosquito larva or a fly maggot. However, by whatever means it came about, there is no question of the fact of adaptation, or that in many insects it has separately modified the young and the adult.

Structural differences between young and adult may have a purely functional basis without involving environmental adaptation. In the reduviid bug *Rhodnius* as described by Wigglesworth (1954) changes that take place at the moult to the adult include completion of the wings and genital organs, the appearance of ocelli, and changes in the texture of the cuticle. Most of these changes are simply the maturing of organs that begin their growth in the young insect. The change from a soft extensible cuticle in the juvenile feeding stage to a hard unstretchable cuticle in the adult, however, involves a differential activity of the epidermal cells in forming first the juvenile cuticle and then the imaginal cuticle. This dual capacity of the epidermis is stressed

by Wigglesworth (1959) as playing an important part in insect transformation generally.

A very simple case of environmental adaptive juvenile metamorphosis is shown by the cicada, in which the young insect on hatching is already modified for an underground life. The adult female cicada, following the tradition of her race, persists in inserting her eggs into the twigs of trees. The newly hatched young have piercing and sucking mouth parts as if they were expected to live on the trees as do their relatives the aphids, but their tiny beaks are too weak to penetrate the bark. The young creatures very soon jump off or drop off the trees to the ground, where they find themselves right at home. They are somewhat cylindrical in form with bluntly rounded heads, and the fore legs have been adapted in advance for digging by the development of strong spinous processes on the femora, and the articulation of the cylindrical tarsi on the mesal surfaces of the tibiae. The young cicadas at once enter some crevice in the ground. After a long subterranean life, feeding on the sap of tender roots, they again come to the surface, now in a more mature form, ascend a post or tree trunk, and transform to the adult. On the shedding of the cuticle it is seen that the front legs have reverted to the normal adult structure. The change evidently has been accomplished by a differential growth of the leg epidermis. Also before the moult other adult organs have matured, and the body has taken on the adult form. The juvenile modification of the cicada would appear to be a relatively recent event, since the adult female, unlike most other insects, does not lay her eggs where the young on hatching will find their proper habitat, but in the trees where the eggs are safer than they would be in the ground.

Among the insects classed as hemimetabolous, juvenile adaptation becomes more complex, but still is of the same nature as that of the cicada, being a temporary modification that fits the young insect for a special environment or way of living.

The aquatic stonefly larva in its general external form resembles the adult; ocelli and compound eyes are present, the mouth parts are of the biting and chewing type. Its principal external adaptation to life in the water is the presence of gills on various parts of the body. The larval musculature, as described by

Wittig (1955), is evidently adapted to the various movements of the larva, and undergoes a considerable reconstruction at the change to the adult. Some muscles of the larva are destroyed, others reduced, some are enlarged, others split into two muscles, and there are shifts in the points of insertion. In the mayfly larva again the chief specialization for an aquatic life is the possession of gills and modifications of the body related to respiration. Here, however, a major difference between the larva and the imago results from the reduction of the mouth parts in the adult, which is short lived and takes no food. The larva thus becomes the feeding stage for the whole life of the individual.

In the Odonata the difference between larva and adult is intensified because the larva is adapted to its aquatic life not only by the development of gills, but by a very special modification of the labium for securing active prey, and by correlated adaptations in other parts of its anatomy. The adult labium is formed by a new growth of the epidermis within the cuticle of the larval labium, and has been shown by Munscheid (1933) to be accompanied by a reconstruction of the musculature, involving the loss of two pairs of the larval muscles. In the larval abdomen there are two sets of muscles, those of one set being special larval muscles destroyed in the adult, those of the other being carried over into the adult to become the principal intersegmental muscles. Other changes between larva and adult involve the construction of the thoracic wing muscles, and a reconstruction of the alimentary canal and tracheal system. As the writer (1954) has noted, " the total reorganization of the dragonfly during its transformation period amounts to a remarkable degree of metamorphosis for an insect commonly said to be hemimetabolous." In other words, the larva is highly specialized for its life in the water.

The holometabolous insects differ from the hemimetabolous forms in the presence of a reconstructive stage called the pupa, which has been explained as meeting the need for making new muscle attachments. Yet in the simpler forms of holometabolism changes from larva to adult are hardly equal to those that take place in the dragonfly. In the megalopteron *Sialis*, for example, as described by Ochsé (1944), the principal adaptive organs of the larva are the abdominal gills and caudal filament, which are

lost at the change to the pupa. In the pupa there is formed from newly appearing myoblasts a thin layer of imaginal muscles along each side of the abdomen, but the other tissues go over unchanged from the larva, and are therefore "larvo-imaginal." The larva of the related *Corydalus* is aquatic and provided with gills, but has little other external adaptation to life in the water. The general muscular system is said by Kelsey (1957) to "maintain its identity throughout the larval, pupal, and adult stages." However, a few muscles are found only in the larva, and some of the wing muscles of the adult are formed in the pupa. Other changes between larva and imago, such as the lengthened antennae and mandibles of the latter, are adult specializations.

From these examples it would appear that holometabolism had a simple beginning, and that the nature of the larva is in no way different from that of insects without a pupal stage. In the higher orders, however, the difference between larva and adult increases until the two are practically two different animals developing from one egg.

Among the Holometabola it is evident that specialization of the adult has had much to do with the aberration of the young from the parental structure. The moths and butterflies, for example, have developed a proboscis for feeding on nectar, a highly inadequate diet. It becomes the duty of the larva, therefore, to provide the essential food elements for the whole life of the individual, and the structure of the caterpillar is in almost every way an adaptation for finding, consuming, digesting, and storing a great quantity of food.

The wingless young mosquito could not follow the blood-sucking habit of its mother, or the nectar-feeding of its father. Hence it has taken to the water where it has acquired a body structure suitable to aquatic life, and has developed a very special feeding mechanism of its own. Likewise in other orders adult specialization has left the young to their own devices, and juvenile evolution has provided them the means of living an independent life. The ants, wasps, and bees furnish a home and food for their offspring, which left alone would be quite helpless. The question of the time relation between the beginning of adult specialization and juvenile specialization is one that would be too difficult to discuss.

Because of the structural disparity that has come about between the young and their parents in the holometabolous insects, the transformation from larva to imago becomes doubly complicated by reason of the larval characters that have to be discarded, and adult characters that must be newly built up.

The degree of reconstruction that takes place in the pupa depends on the structural divergence between larva and imago. A new cuticle must always be laid down for the adult. In some insects, as in Coleoptera, it may be formed by a differential action of the cells of the general epidermis, but in higher orders a new epidermis is formed from groups of regenerative cells, while the old cells degenerate and are thrown off into the body cavity. In the same way the ectodermal parts of the alimentary canal may be enlarged by regrowth of the cells, or reformed from regenerative centers at their inner ends. The wall of the mesenteron, on the other hand, usually goes into dissolution, and is replaced from groups of regeneration cells. The larval muscles may go over into the adult with simple modifications, but when the larva acquires a special musculature of its own, this musculature completely disintegrates, and new muscles are formed for the adult from undifferentiated myoblasts. Organs such as the heart, the tracheae, and the nervous system that must be functional through the pupal period commonly go over into the adult with little change, but even these organs may undergo considerable modifications to meet the needs of the imago.

Though the transformation of the larva into the imago is commonly called " the metamorphosis " of the insect, there appears to be little actual transmutation of larval tissues into adult tissues. An example of true metamorphosis should be the change of water into ice, it is still H_2O that has merely changed its form; or perhaps an anatomical example is the change of cartilage into bone. The so-called metamorphosis of the larval insect into the imago is not a change of this kind. Epidermal cells that form first a larval cuticle and then an imaginal cuticle do not themselves undergo a metamorphosis. As Wigglesworth (1959, p. 71) says, " it is obvious that the capacity to lay down either larval or adult cuticle is latent within the selfsame cell." The cell apparently might be likened to a skilled artisan who

makes two kinds of fabric according to the demands of the market. Only parts that are physiologically necessary for the continuous life of the insect, such as the heart, tracheae, and central nervous system, go over from larva to adult. Otherwise the special larval tissues are destroyed, and the adult is formed by renewed development of latent imaginal tissues.

Tiegs (1922, pp. 494–495) in discussing the change from larva to adult in holometabolous insects says that at times it amounts to "an absolute death—in the fullest sense of the word—of the larva. If imaginal tissues were not present the 'corpse' would be left to decompose; the imaginal cells, however, take the opportunity, and nourishing themselves upon the highly nutritious material of the dead larva, grow by an orderly process of development into a totally different organism—the imago." Even muscles of the imago that replace larva muscles *in situ* are formed in *Nasonia*, according to Tiegs, by imaginal myocytes that penetrate the disintegrating larval muscles. The resulting change of form from larva to adult is thus a "metamorphosis" only in the eye of the beholder. If an old house is torn down to the foundation and a new and different one is built up from the foundation, a beholder might exclaim, "What a metamorphosis!," while actually one house has simply been replaced by another. So with the insects; the caterpillar is not converted into a butterfly, or the maggot into a fly—one replaces the other on the same foundation.

The real metamorphosis of the insect is clearly the change in structure that transformed the young insect into a specialized larva, presumably resulting from favorable gene mutations. The insect thus became virtually two animals developing from one egg. The larva, whatever its form, being still the young of its species, takes priority in development, and its structure is preserved by a juvenile hormone until the larva has completed its role in the life history of the individual. Meanwhile, most of the adult development is suppressed until the end of the larval life, when it is resumed and rapidly completed in the pupa. The apparent metamorphosis of the larva into the imago, therefore, is simply the return to the parental form accompanied by the discarding of the specialized larval structures. It is thus not a

process of transmutation, and might appropriately be termed the *retromorphosis* of the insect.

The writer, of course, is under no illusion that the term "retromorphosis" will be accepted by entomologists. For the general public it would completely spoil the sentiment that has been inspired by the idea that the caterpillar, after its death and interment in the pupa, is resurrected as a glorious butterfly. Since the word "metamorphosis" means simply "a change of form," it may be argued that it can refer to any transformation regardless of the nature of the change. Yet, it should be recognized that the change of form that takes place when retromorphosis replaces the larva with the imago is a very different thing from the actual metamorphosis that produced the specialized larva. Two different processes should not be confused under one name. The prefix *retro* does not imply that development goes backward, but that morphogenesis reverts to the adult line of development.

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A NEW GENUS OF WINGLESS GRASSHOPPERS FROM CALIFORNIA RELATED TO BRADYNOTES (ORTHOPTERA; ACRIDIDAE; CYRTACANTHACRIDINAE)

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The *Bradynotes* complex of grasshoppers in the western United States and adjacent Canada includes about 20 described species, all flightless and either totally wingless or with vestigial tegmina. These grasshoppers offer much potential interest from the standpoint of evolutionary development and distributional patterns, since some species are widespread and others are localized. However, only in recent years has more than a beginning been made in the critical analysis of the genera and the determination of practical specific characters. The latest taxonomic contribution, by J. A. G. Rehn (Trans. Amer. Ent. Soc. 78: 101–115, 1952), carried references to earlier papers in a series defining several genera, and a general paper by the same author (Zoogeography, edited by C. L. Hubbs, Publ. 51, Amer. Assoc. Advancement of Sci., pp. 253–298, especially 268–269, 1958) touched upon the relationships and origin of the complex. Clarifying this complex is necessary to a full understanding of the numerous genera comprising the Melanoplini, so often involved in outbreaks and range grasshopper surveys.

Of the species currently in the genus *Bradynotes*, one inhabiting the high Sierra Nevada Mountains of California (*B. satur* Scudder) has as a distinguishing feature the presence of conspicuous protuberances on the male supra-anal plate. A detailed study of specimens from different Sierran localities shows that five species are included in what formerly was generally regarded as *satur*. Furthermore, the five species comprise a cohesive generic unit. Until recent years this work could not have been

Fig. 1. *Hypsalonia miwoki*, female paratype, Sonora Peak, Calif. (Drawn by J. R. Helfer.)

done effectively because of a shortage of material and the unrealized potential of the concealed genitalic parts as taxonomic characters of tremendous value.

The terminology of the concealed genitalia is according to Eades (Ent. News, 72: 141–149, 1961). In the descriptions of the aedeagus, the two pairs of values occupying an erect position, one pair in front of the other, are regarded as dorsal and ventral valves, respectively, because of general custom based on the origin of these structures. However, the surfaces of the values directed cephalad and caudad are referred to as "anterior", "posterior", etc., because of the advantage of applying terms in keeping with the orientation of the preparations. With respect to the proportions given, the mesosternal interspace is measured across its narrowest point with an ocular micrometer,

then the measurement of a lateral lobe is taken at the directly opposite point by taking a reading along the same line.

The genus is confined to the Sierra Nevada subdistrict of the Sierran-Cascade district (Classification of A. H. Miller, An analysis of the distribution of the birds of California, Univ. Calif. Publ. Zool. 50: 531–644, especially 589, 1951). The recorded altitudes at which the genus occurs range from 8,200 to 12,000 feet, though some localities, when the altitude is not given, may be lower. The most northern and southern localities are only about 150 miles apart. With the possible exception of two species (*miwoki*, *tioga*) from an unspecified locality in Yosemite National Park, no geographic overlap of two or more species is known. In view of the very high altitudes and rugged terrain involved, much more extensive collecting might reveal extremely interesting features concerning speciation. In the present study, a total of 176 specimens of the new genus from 18 localities have been examined.

A special incentive for this paper has been the large number of specimens contributed by David C. Rentz of the California Academy of Sciences (CAS). Other important loans have been arranged through Irving J. Cantrall and T. H. Hubbell of the University of Michigan, Museum of Zoology (UMMZ), F. S. Strohecker of the University of Miami, Coral Gables, Florida, and J. R. Helfer of Mendocino, California, who also contributed a drawing of *Hypsalonia miwoki*. Most of the remaining material is from the United States National Museum (USNM) and the Academy of Natural Sciences of Philadelphia (ANSP). As usual, James A. G. Rehn of the latter institution has cooperated in several very helpful ways. The assistance of these persons is appreciated very much.

The following key distinguishes the new genus from *Bradynotes*, from *Hebardacris* which occupies an overlapping Sierran territory, and from *Nisquallia*, which though not overlapping territorially shows close relationship. *Nisquallia* and *Hebardacris* appear to be the closest relatives, demonstrating nearer affinities than *Bradynotes*. Other genera in the complex do not appear to be as closely related, nor do they inhabit the same area. *Asemoplus sierranus* Hebard occurs in Plumas and Sierra

Counties, California, but it is at once separated from the new genus by the presence of small, narrowly oval tegmina.

Key to some Genera of the Bradynotes Complex, mainly from the southern Sierra Nevada Mountains

1. With a well-developed tympanum on each side of abdominal tergum 1; female subgenital plate with strongly angulate lateral lobes (fig. 26); aedeagus with dorsal valves not developed. (Widely, but locally, distributed in far western United States and adjacent Canada) *Bradynotes* Scudder

   Without a tympanum; female subgenital plate with lateral lobes not angulate or, if they are, broadly rounded or obtuse (fig. 27); aedeagus with dorsal valves well developed 2

2. Male supra-anal plate with strong dorsal protuberances (figs. 35–39); female supra-anal plate usually with a distinct transverse carina about midlength; metasternal interspace of male about as wide as a lateral lobe. (Sierran regions of California, from Placer to Inyo Counties) ..... *Hypsalonia,* new genus

   Male supra-anal plate lacking dorsal protuberances; female supra-anal plate without a distinct transverse carina, though it sometimes is suggested at lateral margins; metasternal interspace of male narrower than a lateral lobe 3

3. Lateral facial carinae strongly developed; furcula absent; ventral valve of ovipositor with basal tooth. (Olympic Peninsula of Washington) *Nisquallia* Rehn

   Lateral facial carinae obsolete; furcula present, but small; ventral valve of ovipositor without basal tooth. (Southern part of Sierra Nevada Mountains of California, mainly Inyo, Fresno and Tulare Counties) *Hebardacris* Rehn

HYPSALONIA, new genus

Generic description.—General form much like *Bradynotes.* Head with interocular distance on vertex decidedly less than width of one eye in dorsal view (male), slightly less to slightly greater than width of one eye (female); eyes somewhat more prominent and bulging than in *B. obesa;* lateral carinae bordering fastigium ranging from scarcely indicated to moderately prominent; disk of fastigium scarcely to moderately sulcate, strongly declivant ventroanteriorly; frontal costa with variable sulcation, with from little to no narrowing at junction with fastigium, usually with scarcely any indication of a transverse carina separating costa from fastigial depression; frontal costa in profile weakly and very broadly protruding between antennae; lateral facial carinae obsolete or moderately well developed.

Pronotum with disk about as long as wide, without definite lateral carinae, with low irregular bosses at shoulders of prozona, median carina distinct on metazona, obsolete on prozona, anterior margin truncate, posterior margin frequently with trace of emargination; lateral lobes with

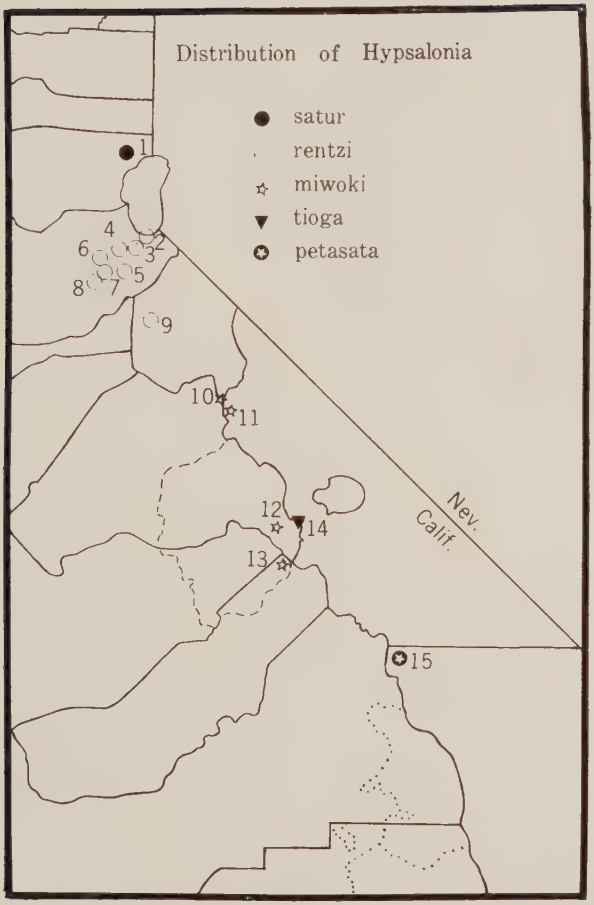


Fig. 2. Map of Sierran section of California, showing distribution of *Hypsalonia* spp. Counties in solid outline, Yosemite National Park in dashed lines, Kings Canyon and Sequoia National Parks in dotted lines. Numbered localities as follows: 1. Squaw Peak; Five Lakes Valley; 2. Tallac; 3. Fallen Leaf Lake; 4. Glen Alpine Creek; 5. Upper Echo Lake; 6. Devils Basin; 7. Ralston Peak; 8. Strawberry Valley; 9. Winnemucca Lake; 10. Sonora Peak; Sonora Pass; Upper Deadman Creek; 11. 3 miles south of Sonora Pass; 12. Tuolumne Meadows; 13. Mt. Lyell; 14. Saddle between Dana and Gibbs Peaks; 15. Near Mono Pass, northwestern Inyo County.

ventral angles varying from broadly conelike to obsolete; minimum width of mesosternal interspace varying from subequal to moderately more than opposite width of one lateral lobe (male), decidedly more (female); metasternal pits about as distant as opposite width of one lateral lobe or slightly more (male), much wider (female); tegmina and wings entirely absent; hind femur slightly less robust than in *Bradynotes;* dorsal spines of hind tibia 6–7 (lateral), usually 8, rarely up to 10 (mesal).

Abdomen with tympanum absent; furcula of male absent or minute; cerci very short, about as long as basal width, apex very blunt or acute with about a 70° angle; supra-anal plate with conspicuous dorsal protuberances arranged transversely a little basad of the middle (male), usually with a transverse carina, strengthened near lateral margins of disk (female); paraprocts usually with a submarginal carina near apex (male), unspecialized (female); subgenital plate short and broad, the apex unspecialized (male), trigonal produced mesally at apex, lateral lobes usually with obtuse shoulders of about 120–150° angles (female); ventral valve of ovipositor without a basal tooth; dorsal valve with dorsal margin straight to gently upcurved in apical half.

Concealed male genitalia with lateral lobes absent, cingulum with apodemes rodlike but flat, rami long and narrow with anterior margin flared laterally, the ventral limit of the flared portion marked by a small lobe, rami with a mediodorsal process almost reaching to point where arch fuses with sheath, central membrane transverse, slitlike, sheath not overhanging dorsal phallotreme cleft, part of sheath developed as lateroventral coriaceous raised regions; dorsal and ventral aedeagal valves elongate and extending dorsally conspicuously; ventral aedeagal valves each consisting in large part of a highly distinctive sclerotized portion, tubelike in cross section, extending to the innermost part of sheath, and continuous with the dorsal aedeagal sclerite at the basal end of the lateral phallotreme groove; ventral aedeagal sclerites articulating with endophallic plates; endophallic apodemes not strongly flared laterally. Epiphallus large and heavily sclerotized, bridge narrow, depressed; lophi large, diagonal in dorsal view; ancorae present as well-developed hooks; very weakly sclerotized areas present both mesad and laterad of the ancorae; oval sclerites present.

Spermatheca of female with slender, relatively short and nonspecialized apical diverticulum; a much longer, abruptly doubled preapical diverticulum, its basal portion of approximately uniform diameter, borne by a long, very slender spermathecal duct.

A few characters separating *Hysalonia* from *Bradynotes,* additional to those in the key to genera, may be emphasized. The cercus of male *Bradynotes* is elongate, much more tapering than in *Hypsalonia,* and frequently curves ventrally near the apex; in the female it is acute at the apex and is also longer than the basal width. Though variable, *Bradynotes* frequently has a

basal tooth on the ventral valve of the ovipositor, unlike *Hypsalonia*. The aedeagal valves and sclerites and the female spermathecae of the two genera are very different. Slifer (Jour. Morph., vol. 67, p. 221, pl. 3, fig. 30, 1940) illustrated the spermatheca of *Bradynotes*.

The name is adapted from two Greek words, "hypsi" (on high) and "aulon" (pass, defile), in allusion to the high altitudes where this genus occurs.

Genotype.—Hypsalonia rentzi, new species.

Key to Species of Hypsalonia, based on Males

1. Aedeagus with dorsal valve shorter than ventral valve (fig. 43), and ventral valve not knobbed in lateral view; protuberances on supra-anal plate broadly transverse and dorsally inclined as a shelflike ledge (fig. 38); small furcula present. (Vicinity of northern part of Lake Tahoe) ..... *satur* Scudder

   Aedeagus with dorsal valve as long as or longer than ventral valve (figs. 41, 45, 47) or, if not, the ventral valve is roundly knoblike (fig. 49); protuberances less clearly transverse, with maximum development near each lateral margin of disk, and without such a well-defined shelflike ledge (figs. 35–37, 39); furcula absent or very small .. 2

2. Aedeagus (figs. 46, 47) with ventral valve expanded laterally, caplike; protuberances on supra-anal plate sharp and with their lateral margins virtually longitudinal (fig. 35, *lm*); paraproct without submarginal apical carina. (Vicinity of Mono Pass, northwestern Inyo Co.) *petasata*, new species

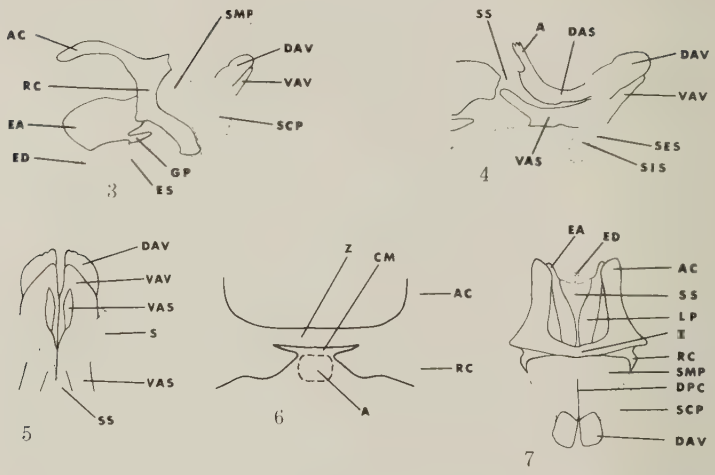
   Ventral valve of aedeagus not caplike at apex; protuberances rounded and with their lateral margins not longitudinal; paraproct with a submarginal apical carina 3

3. Aedeagus with dorsal valve protruding anteriorly at apex (fig. 45); lateroposterior angle of pronotum broadly rounded (fig. 31); body densely pilose. (Vicinity of southeastern Tuolumne Co.) *tioga*, new species

   Aedeagus with dorsal valve not protruding anteriorly at apex; lateroposterior angle of pronotum more sharply rounded (figs. 29, 30); body more sparsely pilose, or scarcely pilose 4

4. Aedeagus with ventral valve knobbed at apex, conspicuously longer than dorsal valve. (Vicinity of southern part of Lake Tahoe, southward to Alpine Co.) ..... *rentzi*, new species

   Aedeagus with ventral valve not knobbed, shorter than dorsal valve. (Vicinity of Tuolumne Co., especially Sonora Pass and Yosemite National Park) ..... *miwoki*, new species



Figs. 3–7. *Hypsalonia miwoki,* male genitalia from KOH preparations, Upper Deadman Creek. 3. Lateral view of phallic complex with epiphallus, basal fold, and ventral infold removed; 4. Lateral view of aedeagal valves and distal portions of sheath and endophallus; 5. Posterior-ventral view of aedeagal valves and distal portions of sheath and endophallus; 6. Posterior-dorsal view of mid-dorsal region of cingulum showing area of fusion to arch; 7. Same as 3, dorsal view. Abbreviations: A, arch; AC, apodeme of cingulum; CM, central membrane; DAS, dorsal aedeagal sclerite; DAV, dorsal aedeagal valve; DPC, dorsal phallotreme cleft; EA, endophallic apodeme; ED, ejaculatory duct; ES, ejaculatory sac; GP, gonopore process; LP, lateral plate; RC, ramus of cingulum; S, sheath; SCP, sheath, coriaceous portion; SES, sheath, external surface; SIS, sheath, internal surface; SMP, sheath, membranous portion; SS, spermatophore sac; VAS, ventral aedeagal sclerite; VAV, ventral aedeagal valve; Z, zygoma.

Hypsalonia rentzi, new species (figs. 2, 14–16, 21, 25, 28, 29, 32, 39, 48, 49)

The distinctive aedeagus readily separates *rentzi* from related species. From *satur*, with which it may be confused because of the closeness of geographic ranges, it also differs in the more angulate ventroposterior angle of the pronotal lateral lobe, as well as the very different protuberances of the male supra-anal plate.

Holotype.—Male. Ralston Peak, California, October 13, 1932 (C. C. Wilson) [U. S. National Museum, Type No. 65773].

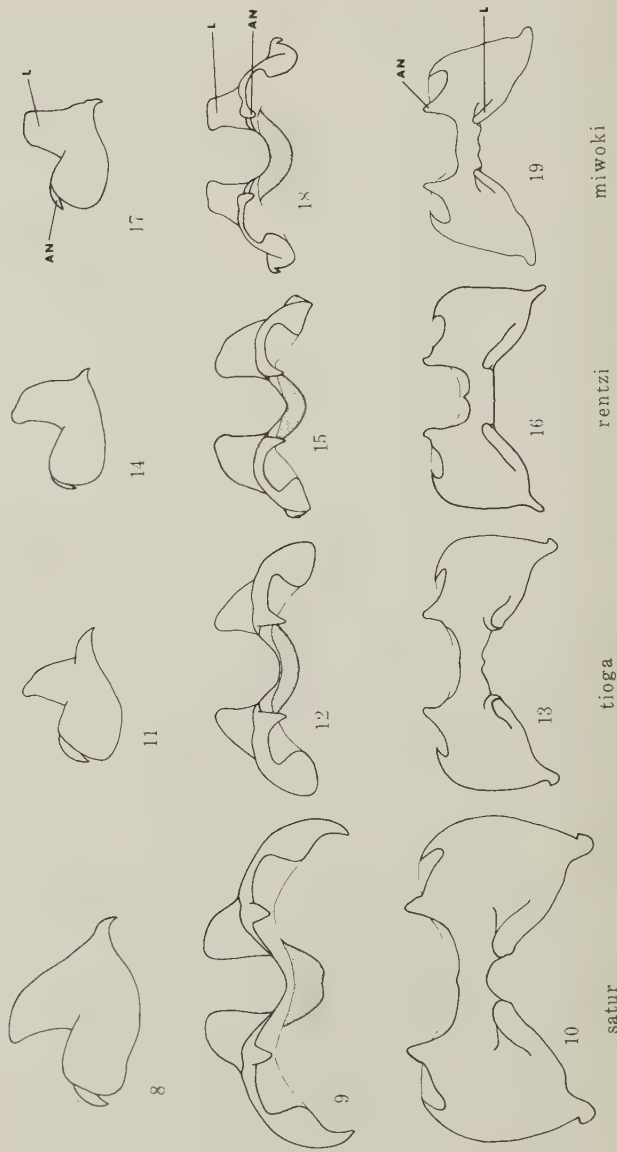
General appearance fusiform, the greatest body width (across mesopleura) three-eighths of body length; surface texture relatively smooth, dull on dorsum, shining ventrally; vestiture inconspicuous, comprising very sparse setae on legs.

Head with dorsal interocular distance less than width of an eye (as 8:14); fastigial depression shallowly sulcate, the bordering carinae rather prominent and abruptly curved mesally opposite anterior margin of eye; frontal costa moderately sulcate, not narrowed at junction with fastigium, an interrupted indefinite carina at juncture; antennae unspecialized, slightly longer than combined length of head and pronotum; lateral facial carinae distinct but not sharp; width across eyes in frontal view less than width across genae (as 35:40); dorsal level of eyes in frontal view about even with highest level of vertex.

Pronotum with principal sulcus and sulcus anterior to it distinct, extending onto lateral lobes, anterior sulcus also distinct, terminating irregularly in lateral shoulder bosses; anterior margin slightly sinuate, posterior margin with trace of median emargination; lateral lobe (fig. 29) with ventroanterior angle well rounded, ventroposterior angle approaching a right angulate condition in lateral view, strongly flaring laterally in dorsal view; prosternal process obsolete; minimum width of mesosternal interspace (fig. 32) in proportion to opposite width of a lateral lobe as 13:10; metasternal pits a little closer than opposite width of a lateral lobe (as 11:13); front femur slightly shorter than pronotum, middle femur a little longer than pronotum, both robust; hind femur moderately robust, extending a little posterior of apex of abdomen, ventral portions of chevron marks in paginal area more prominent than dorsal portions, longitudinal carina marking ventral margin of paginal area prominent.

Abdomen with apex moderately curved dorsally; cercus in lateral view broadly triangular, lateral margins equal to basal width, apex blunt; furcula absent; supra-anal plate (fig. 39) broad, a distinct median longitudinal groove in basal two-fifths; a broad shallow depression medianly and laterally on each side in apical half; dorsal protuberances prominent, making a posterior angle of about 70° with disk (seen in lateral view), lateral margins well rounded, main protuberances not acute, mesal margins distinctly ledgelike nearly to midline; paraproct with well-rounded subapical carina.

Concealed genitalia with dorsal aedeagal valves simple, extending dorsally a little more than half as much as ventral aedeagal valves; latter distinctly and broadly knobbed in lateral view, well separated in posterior view (figs. 48, 49), each ventral aedeagal valve composed entirely of sclerotized portion except for lateral and posterobasal parts; arch moderately long; dorsal aedeagal sclerites relatively fine; anteroventral corner of endophallic apodemes rounded off. Epiphallus with lophi much developed dorsally, dorsal extremities of lophi more horizontal than in KOH preparation of paratype (figs. 14–16).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rentzi
tioga
satur

Coloration.—Dull and inconspicuous; dorsum mainly grayish brown, with some pale mottling; venter pale yellowish brown; hind femur with 3 transverse dark bars dorsally, extending onto dorsal portion of paginal area, ventral border of paginal area a moderately conspicuous pale line, bounded ventrally by dull grayish maroon, ventral surface and ventral half of mesal surface orange red; hind tibia dull yellowish brown, spines tipped with brown.

Measurements (in millimeters).—Length of body, 17.0; antenna, about 7.0; pronotum, 3.1; hind femur, 9.4; front femur, 3.5; greatest width of pronotum, 6.0; hind femur, 2.6; front femur, 1.2.

Allotype.—Female, same locality as type, altitude 9,200 feet, July 24, 1931 (E. O. Essig) [U. S. National Museum].

Differing from holotype as follows.—General build wider and more robust; eyes decidedly less bulging; dorsal interocular distance equal to width of an eye; width across eyes in front view compared to width across genae as 40 : 49; level of eyes in frontal view clearly below highest level of vertex. Narrowest width of mesosternal interspace compared to opposite width of lateral lobe as 27 : 17; metasternal pits much more distant than width of a lateral lobe (as 29 : 23). All femora slightly less robust than in male.

Cercus short, the apex more broadly rounded; supra-anal plate slightly more slender than as drawn from a paratype (fig. 25), a transverse carina of almost uniform prominence but little intensified at lateral extremities; paraproct simple; subgenital plate much as shown for *satur* (fig. 27); dorsal ovipositor valve (fig. 28) but little curved dorsally; spermatheca not examined, but drawn from a paratype (fig. 21, KOH preparation) showing a slender apical diverticulum and a long doubled preapical diverticulum.

Coloration.—Agrees well with male except that dark transverse bars on hind femur are not present on paginal area or lateral part of dorsum.

Measurements (in millimeters).—Length of body, 21.0; antenna, about 6.0; pronotum, 3.5; hind femur, 10.8; front femur, 3.4; greatest width of pronotum, 7.6; hind femur, 2.8; front femur, 0.9.

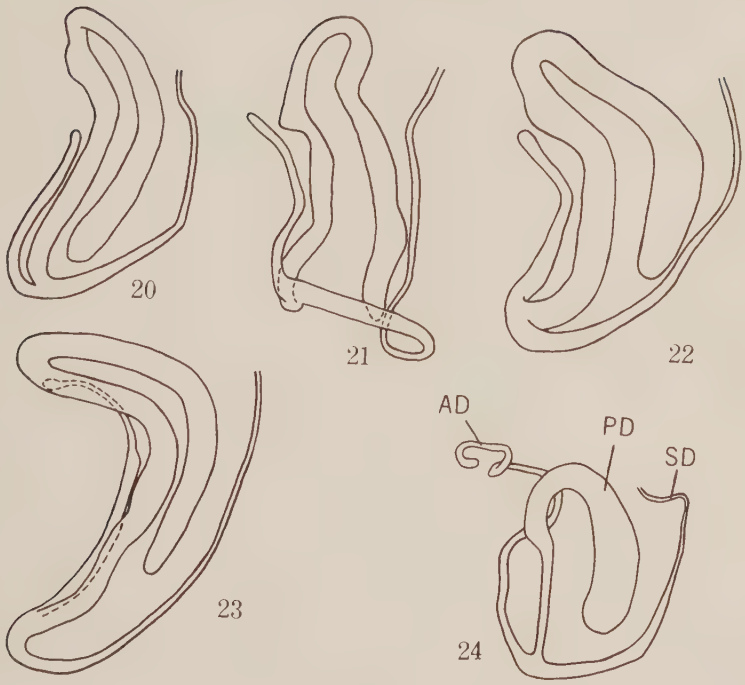
Figs. 8–19. Top, middle, and bottom rows representing lateral, anterior, and dorsal views, respectively, of epiphallus, KOH preparations, of *Hypsalonia* spp. 8–10. *H. satur,* Squaw Peak; 11–13. *H. tioga,* Type locality; 14–16. *H. rentzi,* Ralston Peak; 17–19. *H. miwoki,* Upper Deadman Creek. Abbreviations: AN, ancora; L, lophus.

Variation.—The ventroposterior angle of the lateral lobe of the pronotum is nearly right angulate in several male and female paratypes. In about half the males the mesal margins of the dorsal prominences of the supra-anal plate become obsolete well laterad of the midline, rather than forming a transverse ledge. In some females the transverse carina of the supra-anal plate is obsolete in the mesal third. Some males have a prosternal spine much more distinct than in the holotype. There is little variation in color which is not attributable to preservation. Dark transverse bars of the hind femur extend onto the paginal area in most specimens.

The paratypes average slightly larger than the type and allotype. Five representative paratypes of each sex have been measured, with results as follows (in millimeters): Length of body, ♂ (17.0–18.1, av. 17.7), ♀ (22.0–27.5, av. 24.4); pronotum, ♂ (3.2–3.4, av. 3.25), ♀ (3.5–4.0, av. 3.78); hind femur, ♂ (9.5–10.4, av. 9.9), ♀ (11.0–12.0, av. 11.38).

Specimens examined.—31 (10 ♂, 14 ♀, 7 juv. Type, allotype, paratypes). California: Tallac (no other data), 1 ♂, 5 ♀, 1 juv. [ANSP]; Fallen Leaf Lake, VII, 13, 14, 15, 1915 (E. C. VanDyke), 2 ♀, 1 juv. [ANSP]; same, VIII, 1915 (L. S. Rosenbaum), 1 ♀, 3 juv. [CAS]; G. Alpine Cr., Tahoe, VII, 28, 1915 (E. P. Van Duzee), 1 juv. [ANSP]; Devils Basin, 8,200 feet elev., VII, 6, 1934 (E. O. Essig), 2 ♂, 1 ♀, 1 juv. [ANSP, Univ. Calif.]; Ralston Peak, 9,200 feet elev., VII, 24, 1931, VII, 26, 1933 (E. O. Essig); same, X, 13, 1932 (C. C. Wilson), 6 ♂, 3 ♀ (holotype, allotype included) [USNM, ANSP, Univ. Calif.]; Strawberry Valley, El Dorado Co. (no other data), 1 ♀ [ANSP]; Winnemucca Lake, Alpine Co., VII, 17, 1949 (R. M. Bohart), mating pair [Univ. Calif.].

More precise locations of several of the preceding localities are as follows: Ralston Peak, El Dorado Co., is located just north of U. S. Highway 50, about 2 miles west of Lower Echo Lake. Tallac is near Al Tahoe at the southern end of Lake Tahoe. Glen Alpine Creek flows into the southern end of Fallen Leaf Lake. Devils Basin, in the area of the Meadley Lakes Reservior, is 4 miles northwest of Ralston Peak and 3½ miles southwest of Fallen Leaf Lake. Strawberry Valley, centering about the village of Strawberry, through which U. S. Highway 50 passes, is about 14 miles southwest of Lake Tahoe. Winnemucca Lake at an elevation of about 9,000 feet, and sometimes known locally as "Roundtop Lake," is about 2 miles south of Carson



Figs. 20–23. Spermatheca of *Hypsalonia* spp., KOH preparations. 20. *H. tioga,* Type locality; 21. *H. rentzi,* Tallac; 22. *H. satur,* Squaw Peak; 23. *H. miwoki,* Sonora Pass; 24. Spermatheca of *Hebardacris albida* (Hebard), paratype, Lone Pine, Calif. Abbreviations: AD, apical diverticulum; PD, preapical diverticulum; SD, spermathecal duct. (Figs. 3–24 drawn by junior author.)

Pass on California Highway 88 and 3 miles northwest of Upper Blue Lake.

Distribution.—The localities where *rentzi* has been taken are all in the high Sierra Nevada Mountains near the southern end of Lake Tahoe. The most southern locality, Winnemucca Lake, is only about 20 miles from Lake Tahoe.

Source of name.—This grasshopper is named for our friend, David C. Rentz, of the California Academy of Sciences, through whose cooperation and diligence in the field many of the specimens of *Hypsalonia* have been assembled.

Hypsalonia satur (Scudder) (new combination)
(figs. 2, 8–10, 22, 27, 38, 42, 43)

1897. *Bradynotes satur* Scudder, Proc. U. S. Nat. Mus., XX: 81, 89–91, pl. VII, fig. 1 (♂, ♀, Placer County, California).

Lectotype.—♂; "Placer Co. Cal."; "Sept."; "A. Koebele Collector"; "Drawn"; "Brad. satur Scudder's Type, 1895" (designated by Rehn and Hebard, Proc. Acad. Nat. Sci. Phila. 60: 77, 1912) [U. S. National Museum].

This most northern species of *Hypsalonia* may best be recognized by the distinctive dorsal prominences of the male supra-anal plate and by the aedeagus. The following descriptive comments are based on a series of specimens.

Male.—Vestiture inconspicuous, setae sparse. Head with dorsal interocular distance compared to width of an eye as 7:12; carinae bordering fastigial depression less prominent but of heavier build than in *rentzi;* ventral portion of lateral facial carinae obsolete, not distinct as in *rentzi;* middle sulcus of pronotal disk subobsolete; lateral lobe of pronotum with ventroposterior angle somewhat more rounded than in *rentzi;* minimum width of mesosternal interspace compared to opposite width of a lateral lobe about as 16:12; metasternal pits about as distant as width of a lateral lobe.

Cercus about as long as in *rentzi,* apex usually broader than in *rentzi* and often with a tiny subapical depression; furcula present as small lobes, more sharply rounded in some males than in lectotype (fig. 38); prominences of supra-anal plate with mesal margins prominent to the cleft at midline, often comprising a rather uniform transverse ledgelike shelf, other times with prominences considerably higher at lateral extremities, but always very broad and with the shelf extending to the midline.

Concealed genitalia with dorsal aedeagal valves much shorter than ventral aedeagal valves, tapering toward apex in lateral view (fig. 43), at base connected to sheath laterally; dorsal aedeagal sclerites represented in dorsal aedeagal valves by ventromedial needlelike shafts so fine as to be easily overlooked, finer than in *rentzi;* ventral aedeagal valves in posterior view with mesal margins overlapping briefly; ventral aedeagal valve well sclerotized except in the distolateral extremity; arch shorter than in *miwoki;* endophallic apodemes with ventral part moderately flared. Epiphallus as in figs. 8–10.

Coloration.—Essentially as in *rentzi.*

Lectoallotype.—Same label data as for lectotype except for "Drawn." (USNM).

Comments based on series.—Female. Dorsal interocular distance about equal to width of an eye; width across eyes in front view compared to width across genae about 33: 38; narrowest width of mesosternal interspace compared to opposite width of a lateral lobe about as 26: 14; metasternal pits much more distant than width of a lateral lobe (about as 27: 19).

Cercus as in *rentzi;* supra-anal plate with transverse carina well developed, the lateral extremities usually prominent; spermatheca (fig. 22, KOH preparation) much like *rentzi.*

Size variation.—As a whole, both sexes considered, *satur* is somewhat larger than *rentzi,* but so far as body length is concerned the differences may partly reflect better preservation of the Squaw Peak series of *satur* than is true of many specimens of *rentzi.* Measurements based on 5 representative specimens of each sex are as follows (in millimeters): Length of body, ♂ (18.5–22.0, av. 20.8), ♀ (24.0–28.0, av. 26.8); pronotum, ♂ (3.4–4.0, av. 3.76), ♀ (3.8–4.5, av. 4.26); hind femur, ♂ (8.7–10.3, av. 9.99), ♀ (10.5–12.0, av. 11.4).

Specimens examined.—17 (9 males, 8 females).

California: Placer Co., Sept. (A. Koebele), 1 ♀, 1 ♂ (lectotype, lectoallotype) [USNM]; same locality and date ("Koebele Collection") [bearing an old unsigned *Bradynotes opimus* label, and apparently not previously recorded, but probably collected with the types], 1 ♀ [CAS]; Squaw Peak, Placer Co., 8,300–8,950 feet elevation at summit, VIII, 31, 1910 (Rehn & Hebard), 8 ♂, 5 ♀ [ANSP, USNM]; Five Lakes Valley at foot of Squaw Peak, 7,700 feet elevation, VIII, 31, 1910 (Rehn & Hebard), 1 ♀ [ANSP].

Squaw Peak is about 10 miles southeast of Donner Pass, and about 2½ miles west of Squaw Valley Lodge.

Distribution.—H. satur is known only from mountains west of the northern half of Lake Tahoe.

Field notes by Rehn and Hebard are as follows.—Squaw Peak: On flat top, about 10 feet below summit, on ground almost bare, but with a few alpine plants, mullens and grasses, a series of "*B. obesa*" [i.e. *H. satur*] taken. On precipitous upper rock walls there was practically no vegetation; *Circotettix shastanus* common, a few *C. maculatus,* also one "*B. obesa*" [i.e. *H. satur*]. Five Lakes Valley: "On fine glaciated soil, rocky in places, very scant low vegetation, no trees."

Source of name.—The specific name, in Latin meaning "full" or "rich", probably was chosen in allusion to the robust form of the species.

Hypsalonia miwoki, new species (figs. 1, 2–7, 17–19, 23, 30, 33, 37, 40, 41)

The aedeagus is the most distinctive feature of males of this species, but the sharply rounded ventroposterior angle of the lateral lobe of the pronotum and the weakly developed pilosity are especially helpful in separating females from those of related species, especially of *tioga* which seemingly overlaps *miwoki* in distribution. The descriptive comments below apply mainly to those by which *miwoki* differs from *rentzi*.

Holotype.—Male. Upper Deadman Creek [Intersects Highway 108 just west of Sonora Pass] w. side of Sonora Pass, Sierra Nevada Mts., Tuolumne Co., Calif., 9,400 feet elevation, Aug. 22, 1941 (Rehn and Rehn) [Acad. Nat. Sci. Phila.].

Head with dorsal interocular distance in comparison to width of an eye as 6 : 10; frontal costa a little narrowed at junction with fastigium; antennae clearly longer than head and pronotum combined; width across eyes in frontal view compared with width across genae as 27 : 30; level of eyes in frontal view a little ventrad of highest level of vertex; in dorsal view eyes slightly less bulging than in *rentzi*.

Lateral lobe of pronotum with ventral margin much more sinuate in anterior third than in the illustrated paratype (fig. 30), ventroposterior angle slightly broader than in fig. 30; prosternal process prominent but very blunt; minimum width of mesosternal interspace in proportion to opposite width of a lateral lobe as 16 : 10; metasternal pits a little more distant than opposite width of a lateral lobe (as 15 : 12); front and middle femora each longer than pronotum.

Cercus in lateral view with apex a little more broadly rounded; furcula absent; supra-anal plate with prominences much more elevated laterally than mesally, the mesal development low but distinct, main lateral prominence well rounded, the lateral margin of prominence extending anterolaterally; paraproct with distinct subapical carina.

Concealed genitalia (mainly based on preparations from paratypes) with dorsal aedeagal valves thick and fleshy, exceeding ventral valves dorsally; dorsal aedeagal sclerites occupying virtually entire posterior surface of dorsal aedeagal valves; ventral valves much more separated when seen in posterior view than dorsal valves, exposing narrow portions of ventral aedeagal sclerites; ventral aedeagal valve with well-sclerotized portion visible laterally except at and near base; arch moderately long; ventral part of endophallic apodemes moderately flared. Epiphallus (figs. 17–19) with dorsal margins of lophi nearly horizontal.

Coloration.—General color light brown, approaching brown ochre; hind femur scarcely marked with 3 transverse bars on mesal half of dorsal surface, ventral surface and ventral half of mesal surface weak orange red; hind tibia dull yellowish brown.

Measurements (in millimeters).—Length of body (extended by relaxation), 20.0; antenna, about 7.0; pronotum, 3.2; hind femur, 9.4; front femur, 3.7; greatest width of pronotum, 5.7; hind femur, 2.5; front femur, 1.0.

Allotype.—Female. Same data as for holotype [Acad. Nat. Sci. Phila.].

Head with dorsal interocular distance subequal to width of an eye; width across eyes in frontal view compared to width across genae as 33 : 40.

Prosternal process small, more delicate at apex than in holotype; minimum width of mesosternal interspace compared to opposite width of a lateral lobe as 23 : 14; metasternal pits much more distant than opposite width of a lateral lobe (as 26 : 16).

Supra-anal plate with low but distinct, well-rounded prominences near lateral margins; transverse carina subobsolete near midline; other external genitalia about as in *rentzi;* spermatheca (drawn from a paratype, KOH preparation, fig. 23) with a distinctive preapical diverticulum.

Coloration.—General color gray, with area of pale brown and grayish green; small brownish-black spots near posterior margins of most terga; hind femur with dark transverse bars moderately conspicuous, ventral surface and ventral half of mesal surface pinkish red; hind tibia pale yellow.

Measurements (in millimeters).—Length of body, 20.0; antenna, 7.5; pronotum, 3.9; hind femur, 11.0; front femur, 3.7; greatest width pronotum, 7.5; hind femur, 2.8; front femur, 1.1.

Variation.—The majority of paratypes have the ventral angles of the lateral lobes about as in fig. 30, but most of them show the ventral margin more sinuate in the anterior half. Slight individual differences occur in the prominences of the male supra-anal plate, some being somewhat sharper than in fig. 37.

The paratypes are variable in color, some with a ground color approximating brown ochre, others predominantly gray. About one-third of the paratypes have a pink tinge to the hind tibia; the remainder are mainly pale clay yellow. Decompositional changes within the body following death probably have

played an important part in modifying the resulting color of the dry, uneviscerated bodies.

As regards size variation, the holotype is larger than most other measured specimens, though some paratypes from type locality are equally large. Seven representative paratypes of each sex have been measured, with results as follows (in millimeters): Length of body, male (16.4–17.2, av. 16.9); female (21.6–26.7, av. 23.7); pronotum, male (2.7–3.3, av. 2.86), female (3.4–4.0, av. 3.66); hind femur, male (8.3–9.5, av. 8.90), female (10.7–12.0, av. 11.07).

Specimens examined.—107 (52 males, 45 females, 10 juv. Holotype, allotype, paratypes).

California: Sonora Peak, Tuolumne Co., 11,200 feet elev., VI, 12, 13, 1959 (M. Lungren), 2 ♀ [CAS]; Sonora Peak, VIII, 6, 1959 (D. C. Rentz), 13 ♂, 12 ♀ [CAS, USNM, ANSP]; Sonora Pass, Tuolumne Co., VIII, 4, 1948 (P. D. Hurd & J. W. MacSwain), 4 ♂, 5 ♀, 1 juv. [Univ. Calif., CAS, USNM]; Sonora Pass, 9–10,000 feet elev., VII, 16, 1951 (C. A. Downing), 2 juv. [Univ. Calif.]; Sonora Pass, VIII, 1, 1950, VIII, 23, 1957 (M. J. D. White), 11 ♂, 5 ♀, 2 juv. [ANSP, USNM]; Sonora Pass, VIII, 21, 1959 (C. W. O'Brien), 1 ♂, 1 ♀, 1 juv [CAS]; Upper Deadman Creek, w. side Sonora Pass, 9,400 feet elev., VIII, 22, 1941 (Rehn & Rehn), 11 ♂, 9 ♀, 3 juv. (includes holotype and allotype) [ANSP, USNM]; 3 miles s. Sonora Pass, VIII, 4, 1948, 5 ♂, 4 ♀ [Univ. Calif., ANSP, USNM]; Tuolumne Meadows, Tuolumne Co., VIII, 19, 1955 (J. W. MacSwain), 3 ♂, 2 ♀ (includes 1 mating pair) [Univ. Calif., ANSP]; Mt. Lyell, VII, 7, 1935 (E. C. Zimmerman), 1 ♂, 2 ♀ [Univ. Calif.]; Mt. Lyell, 11,000 feet elev., VIII, 27, 1922 (J. R. Sleven), 1 juv. [CAS]; Yosemite Nat'l. Park, 10–12,000 feet elev., VIII, 10, 1931 (Arthur Stupka), 3 ♂, 3 ♀ [UMMZ, USNM].

Distribution.—*Hypsalonia miwoki* is known only from high Sierran localities, extending from Sonora Peak south to Mt. Lyell, a distance of some 50 miles.

The following notes are from the Rehn and Rehn field notebook for the Upper Deadman Creek specimens. "Hudsonian meadow with gentle slopes of broken rock and coarse gravel, chiefly granitic, along stream. Lush meadow area in tall, yellow-flowered composite and similar plants. '*Bradynotes*' very local on broken rocks, some mating, jumping actively and some at times hiding under rocks."

Source of name.—The species is named for the Miwok Indians, a group of Shoshonean stock, which were primarily foothill people living on the western slopes of the Sierras.

Hypsalonia tioga, new species (figs. 2, 11–13, 20, 31, 36, 44, 45)

The conspicuous body vestiture and broadly rounded ventroposterior angle of the lateral pronotal lobe are especially distinctive features supplementing the highly diagnostic aedeagus. General appearance is like *rentzi,* and the following description mainly includes characters by which *tioga* differs from the former more fully described species.

Holotype.—Male. Saddle between Dana and Gibbs Peaks, Tuolumne Co., Calif., 11,800 feet elev., Aug. 5, 1948 (R. Russell) [Univ. of Michigan Museum of Zoology].

Surface of body except on venter very dull, with comparatively (for genus) dense vestiture of grayish setae about ½ mm. long, thicker on body than legs. Head with dorsal interocular distance compared to width of an eye as 9 : 12; carinae bordering very shallow fastigial depression less prominent than in *rentzi,* obsolete opposite lateral ocelli; no trace of transverse carina at junction of frontal costa and fastigium; antenna short, scarcely as long as head and pronotum combined; lateral facial carinae obsolete ventrad of antennal sockets; width across eyes in frontal view compared to width across genae as 35 : 39; dorsal level of eyes in frontal view only a trace ventrad of highest level of vertex.

Disk of pronotum without distinct transverse sulci, an obsolete sulcus one-third pronotal length from anterior margin the best developed; anterior margin with weak median emargination, posterior margin with a trace of median emargination; shoulder bosses and sulci on lateral lobes distinct; lateral lobe with well-rounded ventral angles (fig. 31 of paratype); prosternal process prominent, but short and very blunt; minimum width of mesosternal interspace equal to opposite width of a lateral lobe; distance between metasternal pits slightly more than width of a lateral lobe (as 17 : 15).

Cercus in lateral view subtriangular, with apex rounded; furcula absent; supra-anal plate with each prominence broadly rounded at point of maximum size, the lateral margin gradually curved, a carina extending mesally toward midline better developed than in illustrated paratype (fig. 36); subapical carina of paraproct poorly developed.

Concealed genitalia with dorsal aedeagal valves enlarged apically and protruding anteriorly; dorsal aedeagal sclerite occupying entire posterior surface of each dorsal aedeagal valve, thicker and more rodlike than in *miwoki;* ventral aedeagal valves extending dorsally subequal to dorsal valves, appearing slightly shorter in posterior and slightly dorsal view (fig. 44); well-sclerotized portion extending to and filling apex of ventral valve, but laterally and posteriorly much less complete than in *satur* and *rentzi;* anterior ventral corner of endophallic apodeme flared strongly (for genus) laterad. Epiphallus (figs. 11–13) with dorsal margin of lophus narrowed, inclined weakly lateroventrally as well as posteriorly.

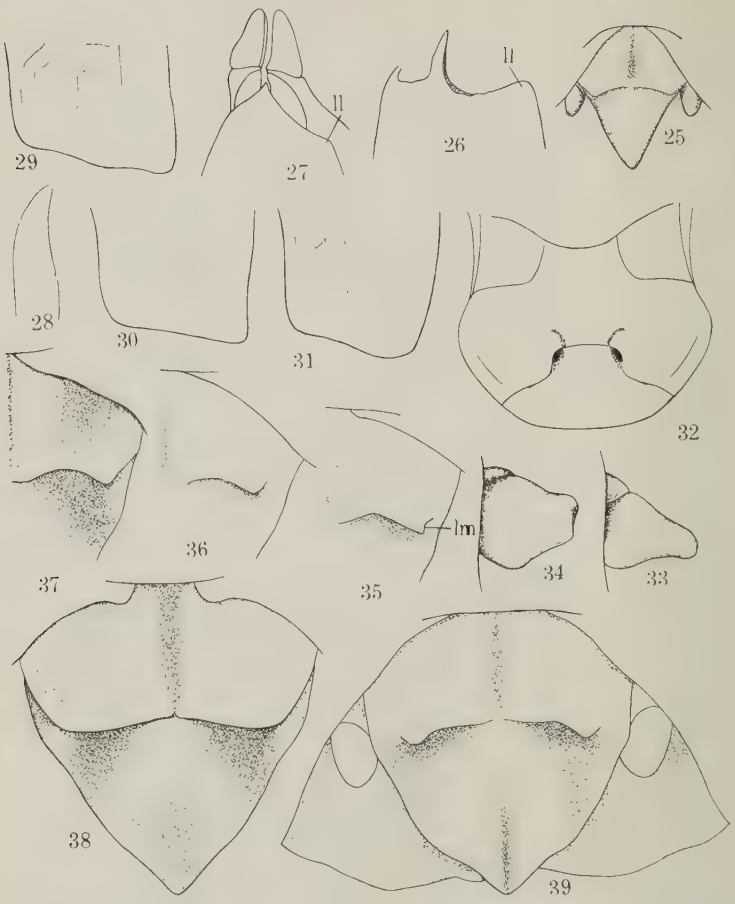


Fig. 25. *Hypsalonia rentzi,* supra-anal plate and cerci, allotype; 26. *Bradynotes compacta* Morse, ventro-lateral view of subgenital plate, showing angulate lateral lobe, paratype female, Ormsby County, Nev.; 27. *H. satur,* ventro-lateral view of subgenital plate and lower ovipositor valves, showing obtuse lateral lobe, Squaw Peak; 28. *H. rentzi,* lateral view of dorsal valve of ovipositor, Winnemucca Lake; 29–31. Left lateral lobe of pronotum. 29. *H. rentzi,* holotype; 30. *H. miwoki,* male, Sonora Peak; 31. *H. tioga,* male, Type locality; 32. *H. rentzi,* ventral view of meso- and metasternum, holotype; 33. *H. miwoki,* cercus, male, Sonora Pass; 34. *H. petasata,* cercus,

Coloration.—General color of dorsum light gray, some mottling of dark gray; venter very pale ochre; eyes light brown; hind femur with blackish-brown transverse bars moderately distinct, ventral surface dull pale clay yellow, tinged with orange on ventral half of mesal surface; hind tibia pale clay yellow.

Measurements (in millimeters).—Length of body, 16.5; antenna, about 5.2; pronotum, 3.0; hind femur, 8.5; front femur, 3.2; greatest width of pronotum, 5.2; hind femur, 2.1; front femur, 1.0.

Allotype.—Female. Same data as for holotype [Univ. of Michigan Museum of Zoology].

Head with dorsal interocular distance slightly greater than width of an eye (as 11 : 9.5); width across eyes in frontal view compared to width across genae as 31 : 37.

Lateral lobes of pronotum much less flared than in *miwoki;* prosternal process scarcely evident, very broad; minimum width of mesosternal interspace subequal to opposite width of a lateral lobe; metasternal pits much more distant than opposite width of lateral lobe (as 24 : 13).

Supra-anal plate with only trace of transverse carina mesally, maximum development of prominences near lateral margins very weak, subobsolete; dorsal margin of dorsal valve of ovipositor with scarcely any dorsal curvature; other external genitalia essentially as in *rentzi;* spermatheca (drawn from a paratype, KOH preparation, fig. 20) with shorter apical diverticulum and more simply curved preapical diverticulum than *rentzi.*

Coloration.—Differing from holotype only in larger patches of dark gray on dorsum of abdomen, and in obsolescence of dark transverse bars on hind femur.

Measurements (in millimeters).—Length of body, 20.5; antenna, about 4.5; pronotum, 3.5; hind femur, 9.2; front femur, 3.2; greatest width pronotum, 6.4; hind femur, 2.4; front femur, 0.8.

Variation.—There is some variation in the density of general body vestiture, perhaps due to wear, and seeing it clearly requires a view perpendicular to the long axis of the setae, in

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holotype; 35–37. Male supra-anal plate, basal two-thirds of right side. 35. *H. petasata,* holotype; 36. *H. tioga,* Type locality; 37. *H. miwoki,* Sonora Peak; 38. *H. satur,* supra-anal plate, lectotype; 39. *H. rentzi,* supra-anal plate, cerci, and paraprocts, holotype. Abbreviations: ll, lateral lobe of subgenital plate; lm, lateral margin of dorsal prominence of supra-anal plate.

strong light. In several males the anterior width of mesosternal interspace is a little wider than a lateral lobe. The slight amount of variation in shape of the ventroposterior angle of the lateral lobe of the pronotum hardly permits any difficulty in separating *tioga* from *miwoki* by this character. Most of the female paratypes have the dorsal prominences near the lateral margins of the supra-anal plate reasonably distinct, though small, more noticeable than in the allotype.

The paratypes from "Yosemite Nat'l. Park" and several of those from the type locality have a general color tending toward brown, rather than gray, probably due in part to changes following death. Very little variation in the color of the ventral surface of the hind femur occurs, but one "Yosemite Nat'l. Park" female shows a weak pink tinge, so the constancy of the yellow color on fresh material is questionable.

The holotype and allotype are slightly smaller than averages obtained by measuring 5 specimens of each sex from the type series. Results are as follows (in millimeters): Length of body, male (15.8–17.0, av. 16.5), female (18.0–22.3, av. 20.4); pronotum, male (2.9–3.2, av. 3.04), female (3.4–4.2, av. 3.66); hind femur, male (8.3–8.7, av. 8.56), female (9.0–11.0, av. 9.72).

Specimens examined.—19 (10 ♂, 9 ♀. Holotype, allotype, paratypes). California: Saddle between Dana and Gibbs Peaks, Tuolumne Co., 11,800 feet elev., IX, 5, 1948 (R. Russell), 7 ♂, 8 ♀ [Holotype and allotype included] [UMMZ, USNM, ANSP]; Yosemite Nat'l. Park, 10–12,000 feet elev., VIII, 10, 1931 (Arthur Stupka), 3 ♂, 1 ♀ [UMMZ, USNM].

Distribution.—Because the second locality above is not precise, only the type locality can be plotted on a map in detail. Furthermore, since specimens of both *tioga* and *miwoki* bear the identical Yosemite Nat'l. Park label, but no more detailed data, it is not known whether both were taken in the same spot and under similar ecological conditions.

Field notes associated with the type locality series, kindly furnished by Irving J. Cantrall, include the comment, "Arctic-Alpine life zone. Bare gravel and rock with scattered grass clumps and small flowers."

Source of name.—The specific name, chosen to suggest the geographic distribution of the species, is from Tioga Pass, located immediately northwest of the type locality.

Hypsalonia petasata, new species (figs. 2, 34, 35, 46, 47)

In addition to the aedeagus, which is distinctive in all species of *Hypsalonia*, *petasata* may be recognized by the sharply angular prominences of the male supra-anal plate.

Holotype.—Male. Near Mono Pass, northwestern Inyo Co., Calif., 12,000 feet elev., Aug. 9, 1959 (D. C. Rentz) [California Academy of Sciences].

Body with inconspicuous vestiture; comparatively large and conspicuously marked.

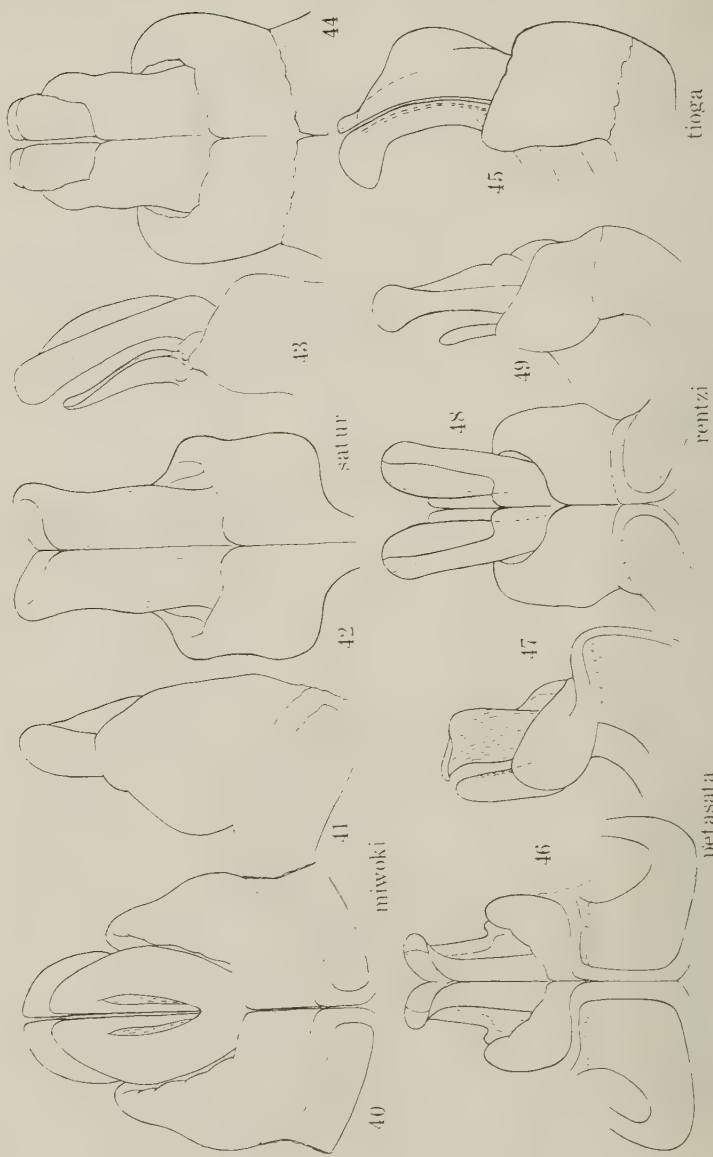
Head with dorsal interocular distance less than width of an eye (as 9 : 12); carinae bordering very shallow fastigial depression less prominent than in *rentzi;* frontal costa with sides gradually and weakly expanding for ventral two-thirds of its length, then moderately and broadly narrowed prior to fastigial juncture, weakly sulcate in ventral half, tumid above; antennae subequal to length of head and pronotum combined; lateral facial carinae as in *tioga;* width across genae as 37 : 43; dorsal level of eyes in frontal view about equal to highest level of vertex.

Disk of pronotum with principal and anterior transverse sulci as in *rentzi*, but middle one interrupted on each side an appreciable distance from midline, then represented crossing midline by a brief sulcus; anterior margin entire; posterior margin with trace of emargination; lateral lobe of pronotum with rounded angles about as in *tioga;* prosternal process low, more broadly rounded at apex than in *rentzi;* minimum width of mesosternal interspace slightly more than opposite width of a lateral lobe (as 13 : 11); distance between metasternal pits slightly less than width of a lateral lobe (as 11 : 13).

Cercus (fig. 34) short, the apex broadly quadrangular; furcula reduced to traces of curvature in the tergal margin at base of supra-anal plate; prominences of supra-anal plate (fig. 35) each sharply developed, its lateral margin directed anteriorly for a short way, then curving laterally; paraproct without a subapical carina.

Concealed genitalia with dorsal aedeagal valves erect, not knobbed, slightly shorter than ventral aedeagal valves; dorsal aedeagal sclerite occupying posterior surface nearly to apex of each dorsal valve; ventral aedeagal valves flaring laterally at apex (fig. 46), creating a caplike form; sclerotized portion lining much of mesal surfaces of ventral valves. Epiphallus with dorsal margin of lophus rounded.

Coloration.—General color pale yellowish ochre, heavily blotched with blackish brown on dorsum; venter unspotted; hind femur with two conspicuous black transverse bars extending ventrally to midline of lateral paginal area, semilunar areas of knees black, ventral surface and ventral half of mesal surface crimson; hind tibia pale yellow; front and middle legs unspotted.


40
41
miwoki
42
43
satur
44
45
tioga
46
47
petasata
48
49
rentzi

Measurements (in millimeters).—Length of body, 19.0; antenna, about 6.0; pronotum, 3.3; hind femur, 10.0; front femur, 3.9; greatest width of pronotum, 5.9; hind femur, 2.6; front femur, 1.2.

Allotype.—Female. Same data as for holotype [Calif. Acad. Sci.].

Head with dorsal interocular distance slightly less than width of an eye (as 11 : 12); frontal costa not sulcate; width across eyes in frontal view compared to width across genae as 35 : 43.

Disk of pronotum with principal sulcus only entire one, middle sulcus represented by short irregular depressions, anterior sulcus briefly interrupted at midline; lateral lobes of pronotum flared about as in *tioga;* prosternal process blunt, well rounded; minimum width of mesosternal interspace much more than opposite width of a lateral lobe (as 25 : 16); metasternal pits more distant than width of a metasternal lobe (as 28 : 18).

Supra-anal plate with conspicuous depression just anterior to obsolete transverse carina at midline, this depression circular posteriorly, then extending to anterior margin of plate as longitudinal depression about half diameter of circle; dorsal prominences represented near lateral margins of plate by inconspicuous curved carinae; (spermatheca not examined).

Coloration.—Very much like holotype except that front and middle legs are predominantly very pale gray.

Measurements (in millimeters).—Length of body, 25.0; antenna, about 7.5; pronotum, 4.3; hind femur, 12.0; front femur, 4.5; greatest width of pronotum, 8.0; hind femur, 3.3; front femur, 1.0.

Specimens examined.—2 (male holotype, female allotype).

Distribution.—*Hypsalonia petasata* is known only from the type locality, which is some 35 miles southeast of Mt. Lyell, the nearest locality for another species of the genus. The type locality, about one and one-half miles north of Mono Pass, is an unglaciated tableland above timberline, at about 12,000 to 12,400 feet elevation, with only a few plants present, and the ground mostly covered with loose granitic sand. The area has been discussed by John T. Howell, "The Florula of Mono Messa"

Figs. 40–49. Aedeagus of *Hypsalonia* spp., non-KOH preparations in alcohol, even numbers dorso-posterior view, odd numbers lateral view. 40–41. *H. miwoki,* Sonora Peak; 42–43. *H. satur,* lectotype; 44–45. *H. tioga,* Type locality; 46–47. *H. petasata,* holotype; 48–49. *H. rentzi,* Ralston Peak). (Figs. 2, 25–49 drawn by the senior author.)

(Wasmann Jour. Biol., vol. 7, pp. 16–21, figs. 1–2, 1947), especially fig. 2 which shows where the specimens of *petasata* were taken.

Source of name.—The specific name is from a Latin word meaning " with a hat on," with reference to the broadened, somewhat capped apex of the ventral aedeagal valves.

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